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SOME QUANTITATIVE ASPECTS OF ALGAL GROWTH IN LAKE MENDOTA¹

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INTRODUCTION

The seasonal fluctuations in the quantities and kinds of phytoplankton in lakes has received the attention of limnologists for many years. For southern Wisconsin lakes, a good general description of the annual phytoplankton cycles of pelagic waters has been presented by Birge and Juday (1922). Causes of these fluctuations have sometimes been explained on the basis of the levels of chemical nutrients, especially phosphorus and nitrogen compounds, which are present in natural waters, though few generalizations of real or supposed biological and chemical relationships have thus far had wide application.

At the present only a limited amount of information has been gained from experimental algal cultures which can be applied directly toward an understanding of the usually different conditions existing in various natural waters. The experiments of Chu (1942), Rodhe (1948), and Gerloff, Fitzgerald, and Skoog

(1950) have, however, been pioneering efforts in this direction. The broader concept of ecological succession of algal species in relation to the nutrients consumed and liberated, which has been discussed extensively by Pearsall (1932), Hutchinson (1944), and Rodhe (1948), among others, has revealed that certain generalizations accounting for algal periodicities are possible, though Hutchinson has emphasized the complexity of these successional phenomena and the necessity of limiting discussions to the simplest situations in individual lakes.

On the basis of present ecological and chemical information, it has been difficult or impossible to account for the sudden and sporadic outbursts of various phytoplankton species, especially the Myxophyceae which often comprise the "nuisance" blooms of eutrophic lakes (Hasler 1947).

The overall seasonal cycles of some of the phytoplankters for the pelagic areas of Lake Mendota have been described by Birge and Juday (1922), but the more diverse quantitative relationships of the phytoplankton at the inlets of rivers and over littoral areas have not been examined heretofore in relation to the possible contributions from these environments to the lake as a whole. Accordingly, the purpose of this preliminary investigation was to ascertain whether phytoplankton fluctuations, especially of the blue-green algae, could have local origins within a lake and what, if any, were the influences of the

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underlying sediments, plants beds, weather conditions, and water movements.

Data dealing with the chemical composition of the water at the times alga collections were made for this study have been described by Emelity and Hanson (1949).

DISTRIBUTION OF ALGAE IN PELAGIC AREAS

Procedure

A study was made of the yearly distribution of phytoplankton in waters over three major depressions of Lake Mendota. Collections were obtained from just below the surface and at a depth of 10 m. at localities designated PB 3, U 3, and M in Figure 1. These collections were designed to yield information on the depth, areal, and temporal distributions of the pelagic phytoplankton content of the lake throughout the year.

In order to evaluate the quantity of

phytoplankton present, a modification of the method described by Gessner (1944) was used to determine the total chlorophyll content of the water samples. Immediately after collection, three-liter samples of water were filtered through a Whatman No. 42 paper with the aid of slight suction. Two-liter samples were occasionally used when the water was very turbid. The filter paper was then washed with several milliliters of boiling water, not to destroy the chlorophyllase as Gessner has suggested, but to aid in breaking up algal cell walls, thus facilitating pigment extraction. After air-drying, the filter paper was placed in a Petri dish and 12 ml. of absolute methyl alcohol was added. The dish was covered and allowed to stand in the dark. After 24 hours the contents of the dish were filtered into a 25 ml. volumetric flask and made up to volume by absolute methyl alcohol washings of the filter paper and

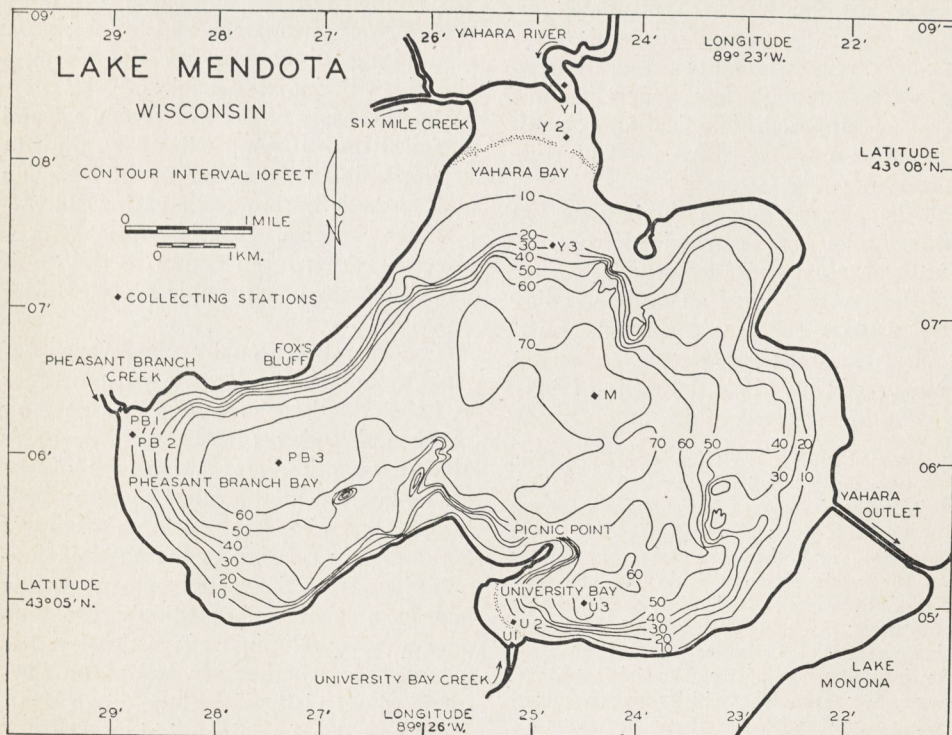


FIG. 1. Map of Lake Mendota, Wisconsin.

TABLE I. Averages of chlorophyll contents in milligrams per cubic meter of surface and 10-meter levels over three depressions in Lake Mendota. Analysis of variance data are given

Season	Date	University Bay U 3	Pheasant Branch Bay PB 3	Central Lake M	Means
Summer stagnation	21 VII 48	5.0	4.2	3.5	4.25
	23 VIII 48	6.0	4.5	3.2	4.58
	27 IX 48	29.0	19.2	37.5	28.58
Means		13.33	9.33	14.75	12.47
Autumn circulation	18 X 48	27.2	31.8	28.8	29.25
	8 XI 48	11.8	10.8	12.0	11.50
	30 XI 48	3.8	3.2	4.2	3.75
Means		14.25	15.25	15.00	14.83
Winter stagnation	4 I 49	5.8	7.5	5.8	6.33
	9 II 49	2.5	2.0	1.8	2.08
	1 III 49	7.2	6.2	4.5	6.00
Means		5.17	5.25	4.00	4.81
Spring circulation	4 IV 49	50.0	42.8	34.2	42.33
	4 V 49	3.5	2.8	2.2	2.83
	23 V 49	7.0	7.0	7.8	7.25
Means		20.17	17.50	14.75	17.47
Yearly means		13.23	11.83	12.13	12.40

Analysis of variance

Source of variation	df	Mean square	F
Dates	11	1062.09	64.447 ^a 61.07
Seasons	3	535.98	32.523 ^a 31.82
Dates within seasons	8	1259.38	76.419 ^a 72.42
Depressions PB 3, U 3, and M	2	13.01	—
Depths	1	9.03	—
Double and triple interactions not involving "dates within seasons"	17	(none is significant)	
Error (all triple and quadruple interaction terms having "dates within seasons")	40	16.48 17.37	

^a Significant at 1% level or less.

contents. The pigment extract was then placed in an Evelyn colorimeter standardized with a methyl alcohol blank; percentage light transmission was measured when a No. 660 filter was inserted. By use of light transmission curves drawn up for known concentrations of chlorophyll-a and chlorophyll-b in the ratio of 3:1, the concentrations of the chlorophyll in mg./l. or mg./cu.m. were obtained. These standard curves had been prepared under the direction of J. F. Stauffer, Department of Botany, University of Wisconsin.

Analysis of results

The chlorophyll contents of the pelagic collections from July, 1948, through May, 1949, expressed as averages of collections at the surface and at a depth of 10 m., are given in Table I. These data are divided into four seasons on the basis of summer hypolimnetic stagnation, autumn circulation, winter stagnation, and spring circulation periods whose durations were determined from vertical series of temperature readings taken throughout the year. It is obvious from a perusal of the

group means in Table I that the depression variability is neither great nor consistent in any one direction. However, from one collection date to the next, there is considerable variation with respect to both the yearly and seasonal means. Further, the seasonal means vary widely about the yearly mean. The analysis of these data is given in the same table with appropriate *F*-tests. (See Snedecor, 1946, for *F*-tables.) The tests of significance indicate that the greatest variations in the chlorophyll contents accompanied temporal differences, while the chlorophyll differences from depression to depression and from surface to 10 m. were not significant.

HORIZONTAL DISTRIBUTION OF ALGAE IN SURFACE WATERS

It is known that large amounts of potential nutrient materials for algal growth are washed into Lake Mendota from inflowing streams (Emelity and Hanson 1949). Just what effect this nutrient influx may have on the quantity at the river mouths and in the weedy littoral beyond the river mouths as compared to the more or less uniform pelagic

areas was the object of this phase of the present study.

Procedure

Yahara, Pheasant Branch, and University Bay areas were studied. Collection stations (Fig. 1) were established at the Yahara River inlet, at the inlet of Pheasant Branch Creek, and at the mouth of the small creek entering University Bay, respectively designated Y 1, PB 1, and U 1; slightly beyond each of these three inlets are dense weed beds where stations are indicated as Y 2, PB 2, and U 2; and farther out in the lake beyond the littoral zone were pelagic stations Y 3, PB 3, and U 3. From July, 1948, through May, 1949, water samples were taken from 0.5 m. at these stations and chlorophyll contents determined.

Analysis of results

Results are given in Table II. In making an analysis of these data, it appeared that the very high chlorophyll contents for some stations, e.g., at the Yahara River mouth, would have an unduly great influence in the analysis of variance. To circumvent such difficulties, logarithmic

TABLE II. Chlorophyll contents in milligrams per cubic meter of surface waters from selected locations in Lake Mendota

Season	Date	University Bay			Pheasant Branch Bay			Yahara Bay		
		River mouth	Weedy littoral	Pelagic	River mouth	Weedy littoral	Pelagic	River mouth	Weedy littoral	Pelagic
		U 1	U 2	U 3	PB 1	PB 2	PB 3	Y 1	Y 2	Y 3
Summer stagnation	16 VII 48	11.5	30.0	40.5	10.0	86.5	13.0	127.0	12.5	20.0
	30 VII 48	14.5	10.5	20.0	9.0	10.5	25.5	56.5	9.0	7.5
	18 VIII 48	14.0	11.5	9.5	8.5	10.0	9.5	56.5	40.5	8.0
	8 IX 48	51.5	18.0	23.0	41.5	26.5	20.0	49.0	18.5	22.5
Autumn circulation	4 X 48	14.5	—	24.5	27.0	28.5	22.0	46.5	19.5	24.0
	25 X 48	20.0	18.0	21.5	21.0	23.0	39.0	75.5	60.0	26.0
	15 XI 48	6.5	4.0	5.0	7.5	36.5	3.5	80.5	33.0	10.0
Winter stagnation	7 XII 48	5.5	5.0	24.5	8.0	24.0	5.5	23.0	16.0	6.5
	11 I 49	5.0	5.0	40.0	8.0	18.5	6.5	4.0	14.0	3.0
Spring circulation	18 II 49	—	4.0	2.5	6.5	6.0	3.0	3.5	5.0	2.5
	11 IV 49	13.0	29.5	42.5	27.5	38.0	49.5	199.0	35.5	27.5
	21 IV 49	11.5	22.5	21.0	14.5	28.0	24.0	194.5	51.0	27.5
	11 V 49	4.5	3.0	3.0	9.5	1.5	2.0	52.0	19.5	9.0
	21 V 49	12.0	10.5	10.5	9.5	10.5	9.0	12.5	7.5	8.0

TABLE III. *Analyses of logarithms of chlorophyll content data given in Table II for Lake Mendota surface waters for three seasons*

Source of variation	Summer period		Autumn period		Spring period	
	df	Mean square	df	Mean square	df	Mean square
Dates (D)	3	0.221952 ^a	3	0.434766 ^a	3	1.292960 ^a
Bays (B)	2	0.088702	2	0.473077 ^a	2	0.608578
Stations (S)	2	0.128680	2	0.075275	2	0.129492
(D x B)	6	0.034766	6	0.058843	6	0.143745 ^a
(D x S)	6	0.056190	6	0.057029	6	0.051758
(B x S)	4	0.260317 ^a	4	0.242241 ^a	4	0.188093 ^a
(D x B x S)	12	0.078397	11 ^b	0.044833	12	0.039853

^a Possibly significant at the 5% level (see text).

^b One df lost due to calculation of missing value.

transformations were made (Bartlett 1947).

The analyses for three seasons only are considered; the winter stagnation season, whose two series of collections are inadequate for analysis, is omitted. Since the seasonal variability has been demonstrated (Table I), these analyses are carried out on an individual seasonal basis as shown in Table III. Though no replicate collections were made, the mean squares of single factors may be compared to the mean squares of the respective two-factor interactions. Correspondingly the two-factor interactions may be compared to the three-factor interaction. There is no error mean square as such.³ The sta-

³ The procedures and justifications for such calculations are summarized by Fisher (1947). The calculations of significant *F*-values may be shown by using letter designations for the appropriate mean squares and degrees of freedom shown in Table III. Using one asterisk to denote possible significance at the 5% level, and two for the 1% level, the following analyses may be shown:

Summer period:

Dates, $F = D/(D \times B) = 6.384^*$.

Bays x Stations, $F = (B \times S)/(D \times B \times S) = 3.320^*$.

Autumn period:

Dates, $F = D/(D \times B) = 7.389^*$, and

$F = D/(D \times S) = 7.624^*$.

Bays, $F = B/(D \times B) = 8.040^*$.

Bays x Stations, $F = (B \times S)/(D \times B \times S) = 5.403^*$.

Spring period:

Dates, $F = D/(D \times B) = 8.995^*$, and

$F = D/(D \times S) = 24.981^{**}$.

Dates x Bays, $F = (D \times B)/(D \times B \times S) = 3.607^*$.

Bays x Stations, $F = (B \times S)/(D \times B \times S) = 4.720^*$.

tistical significance of results obtained by this method are to be considered as suggestive or tentative rather than conclusive.

The three bays were essentially similar quantitatively during the summer and spring periods. During autumn, however, University Bay chlorophyll contents were low enough and Yahara Bay values were high enough to suggest statistically significant differences. For each of the three seasons analyzed, Yahara Bay had the greatest quantity of phytoplankton. The high values of the Yahara River mouth data need not be considered greatly distorted when compared to the values for the remainder of the lake since the drainage into the Yahara Bay is the largest and richest in nutrient materials as compared to the drainage supplied to Pheasant Branch and University Bays.

From river mouths to weed beds to pelagic areas, the bays were individually dissimilar. This condition is reflected in the station x bay interactions which seem to exist throughout the year, apparently caused by the high values at the Yahara River mouth and at the weedy littoral of Pheasant Branch Bay and to the low values at the Yahara pelagic and the University Bay weedy littoral stations. Samples of substrata from the latter two stations had sandy consistency in contrast to the finely divided muds of the other stations.

The date x bay interaction during the spring period means that the relative magnitudes of the chlorophyll contents for

the three bays changed from date to date. Whereas the chlorophyll content at Pheasant Branch showed some tendency to remain intermediate, that of University Bay tended to decrease relatively, while that of Yahara Bay tended to increase as the spring season progressed.

THE POTENTIALITIES OF LAKE SEDIMENTS IN INITIATING AND SUPPORTING ALGAL GROWTH

The work of Lind (1940) and Mortimer (1941-1942) has emphasized the diversities and potentialities of sediments in influencing algal growth from both quantitative and qualitative aspects. With the knowledge that different areas of Lake Mendota support greatly differing quantities of algae, an inquiry into the possible effects of the underlying sediments was instituted.

Cultures of muds taken during the winter

Procedure. From the same three stations in each of the three bays discussed in the preceding section, samples of mud were obtained beneath the ice on 11 March 1949. For each station six 100 g. samples of the sediment were weighed out and strained and washed through bolting cloth (17.4 meshes per cm) using 250 ml. of distilled water. The straining operation served to eliminate the larger aquatic animals and plants, many eggs, and detritus. A microscopic examination of the muds before the experiment showed that practically no actively growing algal forms were present. The chlorophyll contents at this time were, for all practical purposes, negligible, and were considered to be zero. For each of the stations, three of the strained mud samples and the 250 ml. of water were put into clear glass 500 ml. flasks; the remaining three samples were placed in 500 ml. flasks covered with brown wrapping paper. The purpose of the covering was to determine if any species of algae grew better in limited light. The 54 cotton-stoppered flasks, six each from the nine stations, were placed at random on a greenhouse bench, and

were kept fairly near 20° C. with normal daylight as the only light source.

After one week very dense blue-green alga scums began to appear in the flasks whose contents were derived from the river mouth sediments, and at the termination of 18 days there was at least a slight growth in all the flasks. Each flask was polished to remove algae adhering to the glass and, after shaking thoroughly, a 100 ml. portion of the uniform mud and alga suspension was withdrawn from each flask for determination of chlorophyll content. A sample from each flask was examined microscopically for an identification of the species present.

Analysis of results. The results are expressed as averages for triplicate samples of the logarithms of the chlorophyll contents in mg./l. and with the analysis are given in Table IV.

The analysis of these data should be considered from two aspects. First, the mud in any sample may be capable of yielding nutrients which would support algal growth, but it may not contain any algal cells capable of inoculating the culture. Second, the mud may be incapable of supporting algal growth even though a sufficient concentration of cells are present for inoculation. These two aspects taken together are considered, in a crude way at least, to determine the overall potentiality of such a culture to produce algae.

The difference between the clear flasks and the darkened flasks is obvious and would be expected as far as the chlorophyll content is concerned, but the qualitative differences are striking in that the diatoms alone made up the bulk of the algae growing in the darkened flasks. The clear flasks contained not only more diatoms, but also much greater quantities of green and blue-green algae.

Of the bays it is quite obvious that substances in the Pheasant Branch muds initiated the greatest growths. The high values are due principally to blue-green algae.

The station differences are highly sig-

nificant with the greatest yields usually from the river-mouth muds and the least from the benthic muds, though this relationship is not constant from bay to bay.

Accordingly, the bays x station interaction is highly significant owing chiefly to the low yields from the Y 3 and U 2 sandy sediments and to the high yields from PB 1 and PB 3 cultures.

The diversities of these cultures are not surprising and experiments of Lind (1940) indicate that even greater qualitative differences might have been expected had the cultures been allowed to stand for a longer period, or had more samples been used from the same area. The identification of the blue-green algae, especially those forms known to produce blooms in Lake Mendota, is of particular interest. In general the bloom forms

TABLE IV. Averages^a of the logarithms of the chlorophyll contents in milligrams per liter of light and dark algal cultures arising after 18 days from 100 grams of sediment (wet weight) secured 11 III 49 from various locations in Lake Mendota during the ice covered period

Source of sediment		Type of culture	
Bay	Station	Clear	Darkened
Yahara	River mouth, Y 1	0.2683	-0.2139
	Weedy littoral, Y 2	0.4008	-0.2173
	Benthic, Y 3	-0.2377	-0.3160
Pheasant Branch	River mouth, PB 1	0.9190	0.4836
	Weedy littoral, PB 2	0.2942	0.1527
	Benthic, PB 3	0.4169	0.1779
University	River mouth, U 1	0.3728	-0.1783
	Weedy littoral, U 2	0.1386	-0.4231
	Benthic, U 3	0.2765	-0.0626

Analysis of Variance

Source of variation	df	Mean square	F
Light	1	1.98240856	106.487**
Bays	2	1.09826719	58.995**
Stations	2	0.30479545	16.372**
Light x Bays	2	0.05093835	—
Light x Stations	2	0.09387691	5.043*
Bays x Stations	4	0.22266289	11.961**
Light x Bays x Stations	4	0.04124946	—
Error	34 ^b	0.01861643	—

^a Means of logarithms of chlorophyll contents for three replicates (the variation among the three replicates is expressed under "error" in the analysis).

^b Two degrees of freedom lost in calculation of missing values.

* Significant at 5% level.

** Significant at 1% level.

were found in greatest abundance in all the Pheasant Branch cultures and also in the cultures from muds of the river-mouth muds of University Bay.

Diplocystis (= *Microcystis*) *aeruginosa*, one of the most common bloom forms in Mendota, was produced by the muds from PB 1 dark, PB 2 light, some from Y 2 light, very much from U 1 light, and from U 2 light cultures. *Aphanizomenon* sp. was found in cultures of Y 3 light, PB 3 light, and U 2 light. *Gloeo-trichia echinulata*, which is often a prominent bloom form in Lake Mendota, was conspicuously absent from the cultures except for possibly a few tentatively identified trichomes from Y 2 light cultures.

Of the blue-green algae not usually associated with pelagic blooms, *Oscillatoria* was present in many of the light cultures, especially in those whose sediments came from the river mouths of University Bay Creek and Pheasant Branch. At times *Oscillatoria* forms obnoxious scums locally at the river mouth areas.

The high chlorophyll values of Y 1 and Y 2 were due principally to various forms of green algae, of which *Scenedesmus quadricauda* colonies and *Ulothrix* sp. filaments are rather characteristic, and to diatoms.

Cultures of muds taken during the spring

Procedure. To ascertain whether the muds taken beneath the ice change with respect to capabilities of initiating and supporting algal growth, the experiment just described was repeated. The sediments were obtained 21 April 1949 from the same nine stations as before, but three weeks after the ice breakup and during the spring circulation period. It was necessary, however, to determine the initial chlorophyll contents of the muds, because a considerable quantity of algae was found in the muds of the shallower regions after three weeks of ice-free conditions. The experiment was set up in the same way as previously described and the chlorophyll contents in mg./l. of the 54 flasks

TABLE V. Averages^a of the logarithms of the ratios of final:initial chlorophyll contents in milligrams per liter of light and dark algal cultures arising after 17 days from 100 grams of sediment (wet weight) secured 21 IV 49 from various locations in Lake Mendota during the spring circulation

Source of sediment		Type of culture	
Bay	Station	Clear	Dark-ened
Yahara	River mouth, Y 1	0.7744	0.6590
	Weedy littoral, Y 2	0.6986	0.4396
	Benthic, Y 3	-0.0693	-0.2063
Pheasant Branch	River mouth, PB 1	1.4311	1.1166
	Weedy littoral, PB 2	0.2329	0.0554
	Benthic, PB 3	0.8025	0.9929
University	River mouth, U 1	0.5011	-0.0741
	Weedy littoral, U 2	-0.2768	-0.4819
	Benthic, U 3	0.7895	0.7814

Analysis of Variance

Source of variation	df	Mean square	F
Light	1	0.42741366	16.796°
Bays	2	1.50650923	59.202°
Stations	2	1.79967718	70.722°
Light x Stations	2	0.14232247	5.593°
Light x Bays	2	0.02982617	—
Bays x Stations	4	1.73640862	68.236°
Stations x Bays x Light	4	0.04668354	—
Error	35 ^b	0.02544713	—

^a Means of logarithms of chlorophyll contents for three replicates (the variation among the three replicates is expressed under "error" in the analysis).

^b One degree of freedom lost in calculation of missing value.

° Significant at 1% level.

determined after 17 days. Microscopic examination of the algae in the muds was made before and after the 17-day period.

Analysis of results. Because of the decrease in chlorophyll in some of the flasks and because of the different initial concentrations, it was necessary to express the results as ratios of final:initial concentrations. The means of the logarithms for triplicate samples are given in Table V with a statistical analysis. The negative values indicate a decline in the quantity of algae initially present so these results are not strictly comparable to those of Table IV. These declines in many of the darkened flasks and in the clear flasks containing sandy sediments from Y 3 and U 2 are somewhat complicated. It is quite possible that water action during spring circulation could remove finely di-

vided sediments and/or algal cells from such a coarse type of substratum more readily than it would from the more consolidated fine sediments from the other stations. Data on the paucity of adsorbed cations on a sandy lake soil compared to finer soils have been given by Wohlschlag (1950).

Differences between the clear and darkened flasks were about the same as those of the preceding experiment, with the blue-greens predominating in the clear flask cultures, while the diatoms predominated in the darkened flasks.

The highly significant difference among bays was again caused by the high chlorophyll content of the Pheasant Branch stations, but University Bay had the least, whereas Yahara had the least in the earlier experiment. Blue-green algae appeared in the Yahara Bay stations after the spring turnover in increasingly greater quantities and were responsible for this shift.

The station differences, also highly significant, follow the overall pattern described for muds taken beneath the ice. The relative magnitudes of the chlorophyll contents of muds from stations within the individual bays did not compare exactly with the contents of the earlier experiment, however.

Because of the decrease in algae from Y 3 and U 2 sandy sediments, and because of the great increases from PB 1 and PB 3 substrata, the station x bays interaction is nearly identical with the former experiment.

The light x stations interaction is very significant principally because of the high increase in chlorophyll values from river mouth muds in clear flasks and because of the decrease in chlorophyll associated with sediments from the weedy littoral in darkened flasks.

To help explain some of these quantitative differences, a microscopic examination of the cultures showed that again the increases were associated with blue-green algal forms known to be bloom producers. *Diplocystis aeruginosa* was found in the

PB 2 mud cultures and *Anabaena* sp. was found in both PB 2 and PB 3 cultures. *Arthrospira* and *Oscillatoria* were found in quantity in PB 3 and PB 1, respectively. From the University Bay area, U 1 produced much *Diplocystis aeruginosa*, *Microcystis incerta*, and also *Anabaena* sp.; these three forms along with *Chroococcus turgidus* occurred in least quantity at U 2 and in intermediate amounts at U 3. *Rivularia* was also found in the U 3 cultures. The Yahara Bay area exhibited the greatest change between the times of the two culture experiments. The diatom prominence of Y 1 cultures of the former experiment was replaced by a prominence of blue-green forms, *Diplocystis aeruginosa*, *Microcystis incerta*, and some *Calothrix*; *Rivularia* and *Diplocystis aeruginosa* were abundant in the Y 2 cultures while in Y 3 flasks small amounts of *Coelastrum microporum*, some *Anabaena* sp., and very little *D. aeruginosa* and *Oscillatoria* appeared. There were small quantities of green algae in the Yahara Bay sediment cultures for this experiment; the greater quantities of the earlier experiment contrast sharply. Diatoms were present in all the cultures of this experiment but only in very small quantities.

CASE HISTORY OF AN INDIVIDUAL
DIPLOCYSTIS (= *MICROCYSTIS*)
AERUGINOSA "BLOOM"

Hutchinson (1944) has stressed the importance of a succession of algal species which lead up to the summer blue-green blooms in that there is evidence of a correlation between the chemical nutrients or growth substances which are left over or released by one stage of the succession and which affect the following stage. He noted that blue-green blooms appear when the level of nutrients is relatively low. The sequence of events in Lake Mendota during the spring of 1949 suggests a possible application of this explanation to a light bloom of *Diplocystis aeruginosa* on 3 June 1949.

On 30 March 1949 the ice cover of the

lake broke up. A diatom irruption dominated by *Asterionella* was initially evident. With the decline of diatoms the lake became the clearest on record. On 12 May the Secchi disc transparency was 9.5 m. at which time the chlorophyll contents of the waters were very low (see Tables I and II), due chiefly to small quantities of a green alga, *Chlorella* or *Palmellococcus*. On 1 June, a stormy day, the chlorophyll analyses for three pelagic stations were 10.5, 9.5, and 10.0 mg./cu.m., respectively, and the Secchi disc reading was 5.0 m. These quantities of chlorophyll were due principally to *Melosira*, *Cosmarium*, and *Ankistrodesmus*. A few scattered cells of *Diplocystis aeruginosa*, not evident as a surface scum, occurred throughout the lake, but locally at littoral stations Y 2 and PB 2 there were, respectively, 10,200 and 32,600 colonies per liter. No colonies were found elsewhere. (Note that the muds from the Pheasant Branch region yielded good cultures of this species several weeks earlier.) All colonies found were bright blue-green and less than 70 microns in diameter. On 2 June, a calm day, the lake had a slightly turbid appearance, not in the least indicative of blooming. The lake definitely bloomed on 3 June. Open water scums were due to *D. aeruginosa* at 32,460 colonies per liter with a diameter of 0.2-1.5 mm. Of this volume of water it was estimated that there were 40-50 aggregations of cells whose average diameter was about 5 mm. A relatively low chlorophyll content of 21 mg./cu.m. on 4 June indicated that these persisting blue-greens have little chlorophyll when compared to values for green algae of similar dimensions. The very small bright blue-green colonies observed on 1 June possessed very little gelatinous sheath material; the 4 June colonies had thousands of smaller cells, were pale green, and had relatively great masses of gelatinous material.

If the chlorophyll content is even a rough indication of the physiological activity of the cells (and a rough measure

of their requirements for nutrient materials), the slow increase in chlorophyll and the rapid increase in bulk could be explained on the basis of release of a relatively low concentration of nutrients, perhaps undetectable chemically, from the sediments at a time when the succession of preceding algal forms had set the stage for the appearance of the blue-green species. That organic and inorganic substances other than P, N, and Si compounds are necessary for algal development, has been suggested by Hutchinson (1944). The importance of sediments as a source of these other nutrients may be indicated by the fact that many experimental cultures of algae are enhanced when soil extracts are added to the synthetic media (Chu 1942; Rodhe 1948).

GENERAL APPRAISAL

The value of the chlorophyll content measurements of natural waters depends upon completeness of removal of algae, completeness of chlorophyll extraction, evaluation of extract color in quantitative terms, and the relationship of chlorophyll content to the quantity of algae *per se*. Critiques of pigment extraction methods and their applications have been presented by Harvey (1934), Gardiner (1943), and Tucker (1949).

The filtration of algal cells from the water samples was regarded as complete, since practically no algae would appear in the filtrates which were allowed to stand as nonsterile culture media for several weeks. Extractions by methyl alcohol have certain advantages for pigments of fresh-water algae (Gardiner 1943), and these extractions were regarded as complete because periodic re-extractions of the contents on the filter papers showed that in no case was any detectible pigment left on them after the initial 24-hour extraction. While the concentration of pigment was measured only with the use of the 660 millimicron filter in the Evelyn colorimeter, it was believed that this procedure gave at least a fair indication of the chlorophyll-a, a pigment

common to all the more abundant algal species. The other common pigments, xanthophyll and carotin, could not be detected accurately due to interference by yellowish coloring matter derived from detritus in the water or from the sediments. In this connection it was encouraging to note that the yellowish extracts from algae-free sediments gave no indication of chlorophyll when the 660 millimicron filter was used.

That the chlorophyll content of a water sample is at best a proximate determination of algal cell content must be emphasized, though chlorophyll contents did agree with the many cell counts made, at least in a semiquantitative manner. On the other hand, cell counts in themselves do not necessarily give an indication of the photosynthetic activity. Furthermore, quantitative comparisons among cell, filament, or colony counts of unlike species appear to be impracticable. Chlorophyll contents do give some indication of the photosynthetic activity of the algae, and though nonspecific they are comparable.

The data on distribution of algae as measured by the chlorophyll contents of pelagic waters over three major depressions in Lake Mendota show definitely that any differences among these areas must be due only to random variation, on the basis of collections at approximately one-month intervals for nearly one year. It is quite likely that differences among pelagic areas and between the surface and 10 m. levels would exist over shorter periods, however. The fluctuations of chlorophyll contents correspond quite well with the phytoplankton counts of Birge and Juday (1922) on both a seasonal and intraseasonal basis. Especially significant is the great temporal variability in algal abundance at a given collecting area. Likewise temporal variability was significantly omnipresent even when controlled experiments were carried out within a period of a few weeks. Some of this variability could probably be accounted for if a better scheme of breaking the year up into seasons or stages could

be instituted using some criterion other than the state of thermal stratification. Hutchinson (1944) used stages of algal succession. In Lake Mendota the stages of algal succession, in part, have not been constant from year to year. A case in point is the presence of several blooms of blue-green algae one year and their absence the next. Unfortunately, at the present time not enough information exists to indicate whether a given blue-green species blooms at a definite successional stage in the summer or whether it occurs at a time with no relation to the succession of other biological events. In the latter instance environmental, rather than successional, phenomena may hold the key to the explanation of the Myxophyceae blooms.

In the comparisons of the three bay areas the consistent individuality which some of the stations within the bays exhibited looms large as an important factor associated with the possibility of a localized origin of blue-green blooms. Such individuality is emphasized even more when it was observed to be persistent through some of the seasonal changes. Furthermore, on the basis of general qualitative observations over the entire lake, it is believed that such individualities are the rule for littoral areas.

The fact that the three weedy littoral areas studied did not have the same relative amounts of algae as compared to the stations adjacent to them provides an interesting example of station individuality. Only the weedy areas of University Bay seem to have low chlorophyll contents such as would be expected if the antagonistic effect of large aquatic plants were operating as they did in the experimental ponds of Hasler and Jones (1949). While organic substances derived from higher plants have been postulated by Schreiter (1928) as inhibitors of algal growth, there is yet no direct proof that such substances exist. Other explanations of the antagonism between higher plants and algae suggested by Hasler and Jones are competition for soluble nutrient

materials and shading effect of the larger plants. Experiments by Pond (1903), Roelofs (1944), and Wohlschlag (1950) have shown that many of the higher rooted plants depend principally upon the substratum and not the water for nutrients. If shading of the water by the aquatics were to reduce algal development, this effect would be expected to apply to plant areas generally, and such a situation did not appear to exist in the three areas studied in Lake Mendota.

The mud culture experiments offer another possible explanation of the diversities and sources of both nutrient materials and algal cells potentially able to initiate algal growth, and especially growth of bloom-forming blue-green algae. Lind (1940) emphasized the property of various sediments to differ quantitatively and qualitatively and noted that the anaerobic cultures tended to produce more Myxophyceae. As far as the production of blue-green algae is concerned, Lake Mendota mud culture experiments, in which the production of algae in flasks aerated by shaking several times daily was compared to the production in more anaerobic unshaken flasks, showed no statistical difference. Mortimer (1941-1942) and Hutchinson (1941) discussed in detail some of the mechanisms by which nutrient materials may be released from the muds and circulated in the lake waters as have Hasler and Einsele (1948) in regard to the liberation of iron and phosphorus.

That the marginal algae of ponds varies with the sediments and that the wind may play an important part in distributing both algae and mud-derived nutrients has been considered by Lund (1942). Some evidence of this sort can be given for Lake Mendota on the basis of chlorophyll determinations and microscopic examinations of shore waters at Picnic Point and near Fox's Bluff on opposite sides of the lake (see Fig. 1). During the months of June and July in 1948 six series of eight water samples, four from each shore, were taken. For five of the six series the Fox's Bluff shore samples were obtained

after that shore had been exposed to wave action due to easterly or southerly winds for at least 48 hours. The chlorophyll contents of the 20 samples from the Fox's Bluff wind-exposed area averaged 20.5 mg./cu.m. as compared to the 20 samples from the relatively calm Picnic Point waters which averaged 12.4 mg./cu.m. For the one series when the Picnic Point region was wind exposed for at least 48 hours, the four samples on this side of the lake averaged 15.0 mg./cu.m. as compared to the average of four samples from the calmer Fox's Bluff shore which was 9.1 mg./cu.m. A microscopic examination of these water samples indicated that both floating and suspended algae were more numerous on the wind-exposed shores.

If wind-induced turbulence of the waters were associated directly or indirectly with the promotion of algal growth, several plausible explanations may be hypothesized. First, the sediments of the shallower waters may be stirred up, releasing chemical nutrients, and exposing sedimented algal spores and other potentially reproductive structures. Second, the turbulence of the surface waters may induce circulation in the supposedly summer-stagnated hypolimnion which could release nutrients derived there to the nutrient poor surface waters; data are needed on this point to help explain, for example, whether the potentially productive muds beneath Pheasant Branch Bay could contribute to algal production in the lake. These two explanations would seem to have a sound basis in terms of circulation of Lake Mendota waters as worked out by Bryson and Suomi (1950). Third, it is possible that turbulence of waters may result in exposure of the existing algal cells to more water with potential nutrients even if these nutrients are at a low level per unit volume of water, though a series of experiments designed to examine this point yielded negative results. Finally, it is possible that a concentration of algae can take place independent of local growth conditions but

dependent entirely upon the nature of the settling velocities of the algae and upon the nature of the natural convection cells occurring in a body of water (Bryson and Suomi 1950; Stommel 1949).

SUMMARY

1. Differences in quantities of algae for widely differing areas of Lake Mendota are very pronounced both seasonally and intraseasonally. Differences are likewise prominent in experiments extending over periods as short as several weeks.

2. Different bay areas and the stream mouth, weedy littoral, and pelagic stations within these bays have characteristic quantities of algae. Certain of the individual stations have characteristics retained from one season to the next; others vary greatly on a seasonal basis. In any case, where station individuality is indicated, it is present over and above temporal variation.

3. Cultures of algae derived from sediments obtained in the winter and in the spring exhibited characteristic differences from bay to bay and from station to station within the bays. In a general way, the same station individualities present in the cultures were present in corresponding collections from overlying waters. Coarse, sandy sediments from the same locale produced more algae when obtained before the ice-free spring circulation period. Prominent blue-green species which appeared in these cultures are mentioned and their possible significance to subsequent blooms in the lake is discussed. The pattern of distribution of agents causing production of algae should be examined within the sediments of the entire lake.

4. In Lake Mendota there is a suggestion that algal concentrations are greater at a littoral area after a 48-hour exposure to onshore winds than at a similar area not so exposed.

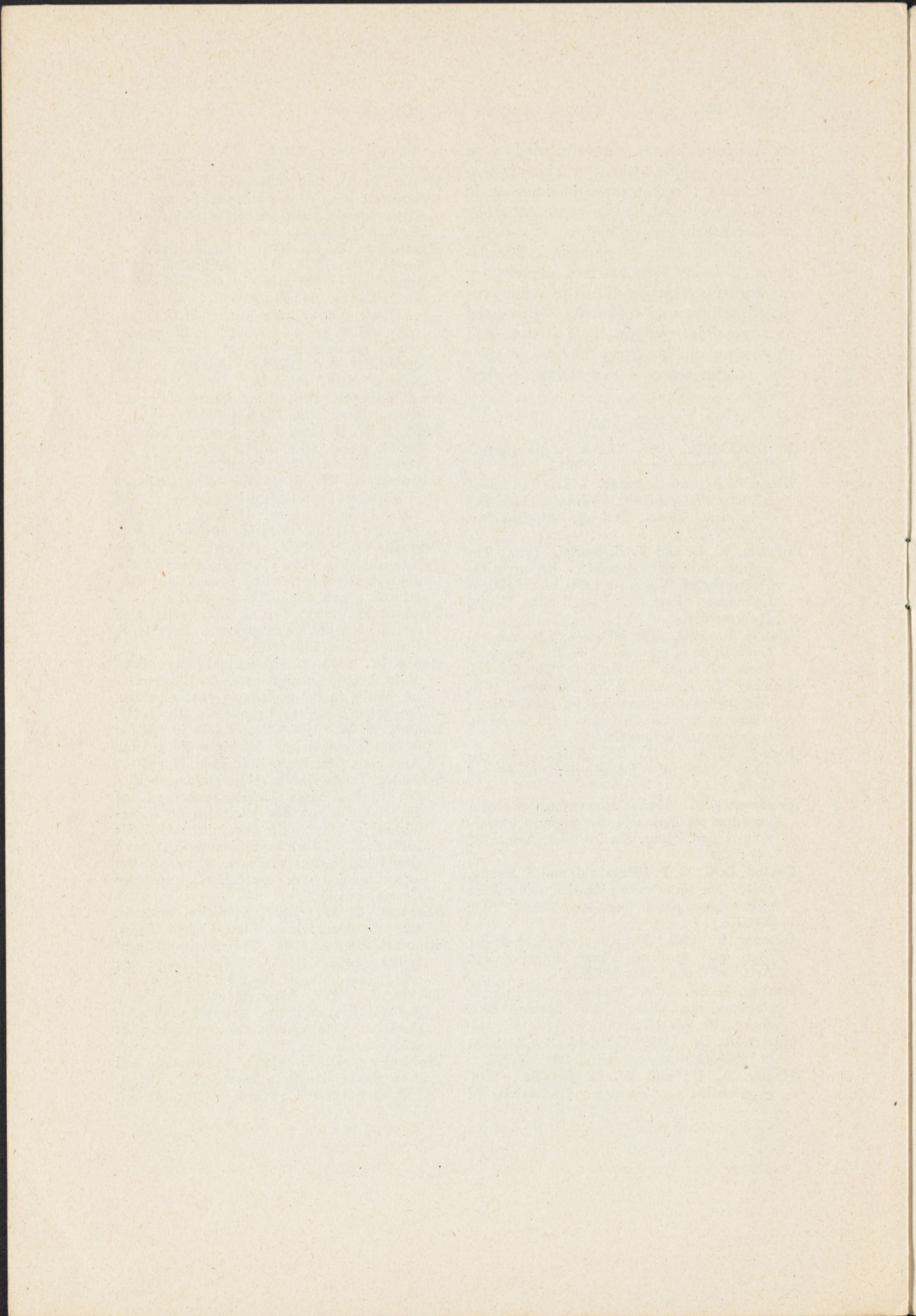
5. A study of chlorophyll, chemical, and microscopic data suggests that the sudden appearance of numerous large colonies of *Diplocystis* (= *Microcystis*) *aeruginosa*

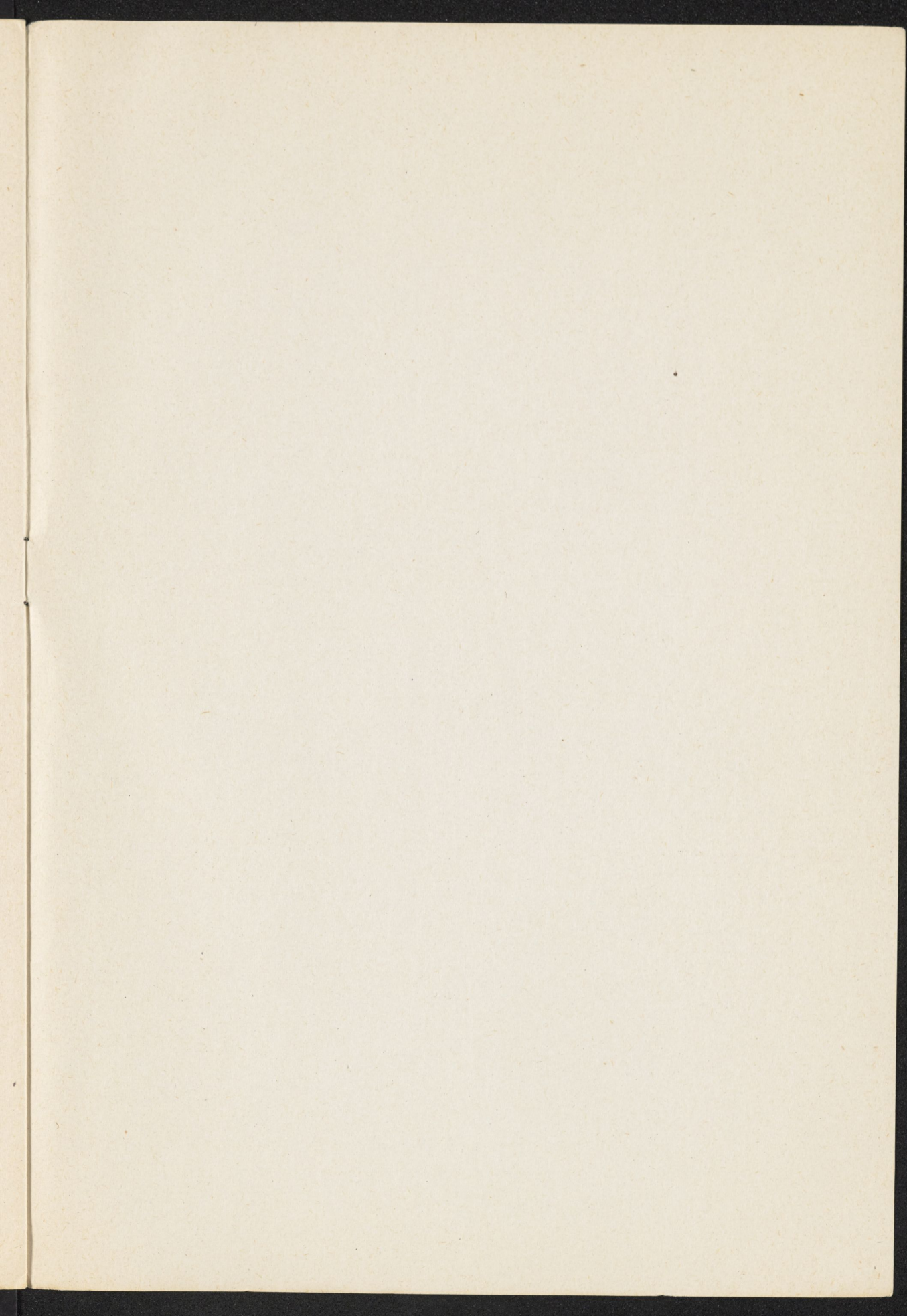
comprising a bloom is accompanied by an increase in gelatinous matter which is proportionately greater than the increase in physiological activity as represented by an increase in chlorophyll.

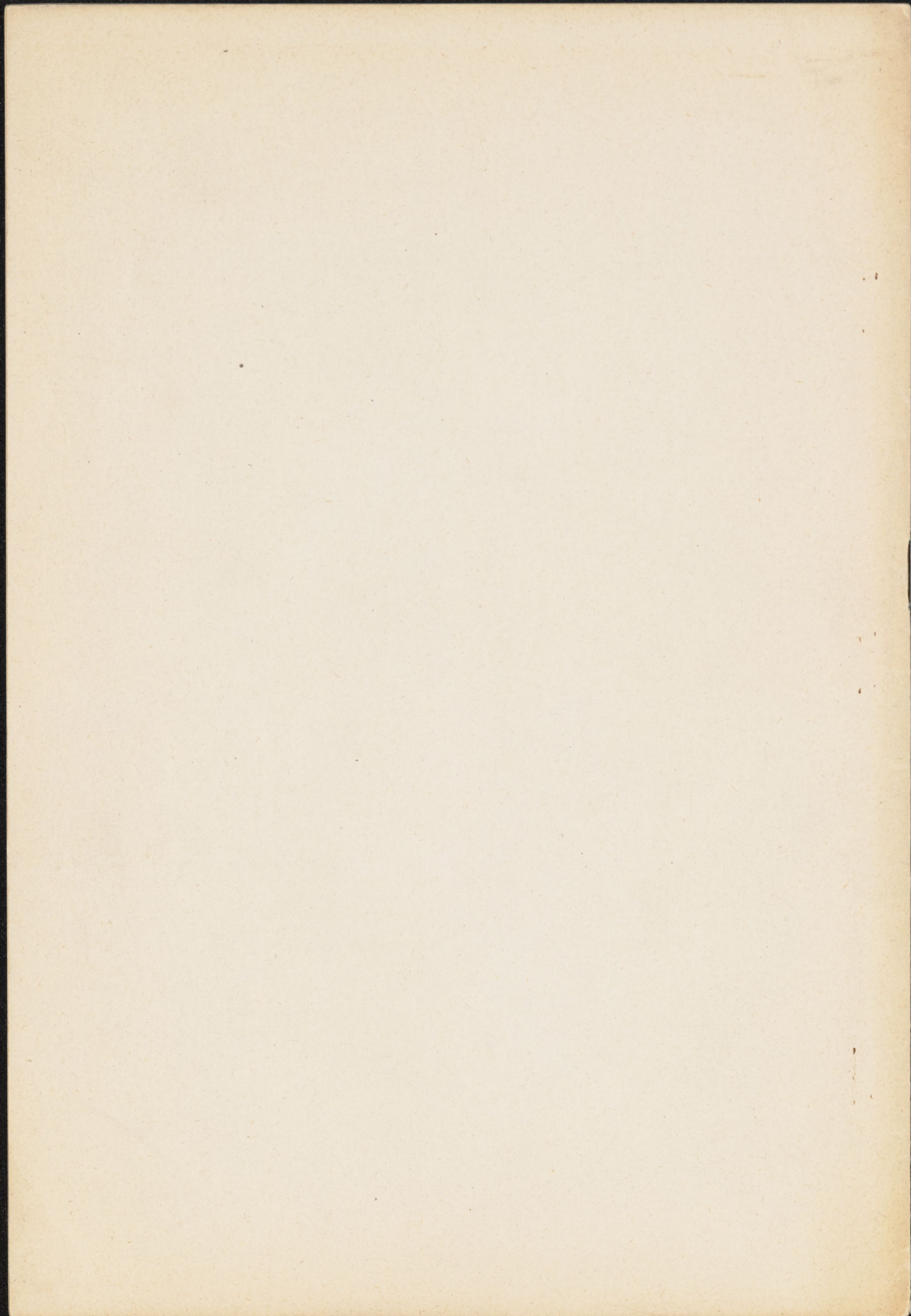
6. On the basis of ecological observations of Lake Mendota and exploratory experiments, the hypothesis of wind produced agitation of sediments is discussed as a possible agent in the initiation and promotion of blue-green blooms in relation to the seasonal succession of algal blooms.

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Factors Influencing the Growth of Phytoplankton

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ABSTRACT

In reviewing the literature dealing with the influence of physical, chemical and biochemical factors on the development and decline of phytoplankton pulses, this paper first outlines the seasonal cycle of phytoplankton pulses which occurs in many parts of North America and then presents evidence that this cycle is caused chiefly by the seasonal change in water temperatures resulting from the change in solar radiation. The way in which this cycle is sometimes obscured by irregular changes in phytoplankton numbers caused by local conditions of weather or nutrient supply is next illustrated. The climate, weather and chemical conditions are then resolved into the components light intensity, duration of illumination, temperature, concentration of nutrients, ionic balance and pH, and these are classified according to specific effects on the growth and survival of plankton algae as limiting, controlling

and lethal factors. The roles of factors originating within the organisms (i.e., autotoxins and antibiotics) are also considered. The discussion of laboratory investigations leads to certain criticisms of present culture methods and to some reinterpretation of observations obtained in some of these investigations. Finally, this paper illustrates the phenomenon of acclimation as it applies to phytoplankton, and it stresses the need for adequate prehistories of culture stocks in order that the results of different investigations can be validly compared.

INTRODUCTION

THE GROWTH of phytoplankton is influenced by factors of supply (limiting factors) and factors of control. Among the limiting factors are the intensity of light and duration of illumination which govern the supply of energy for photosynthesis, and the concentration of nutrient elements which constitute the structural units of carbohydrates. Temperature, ionic balance, concentration of catalysts, and probably pH may be the controlling factors which determine the rate at which phytoplankton can exploit the limiting factors.

At certain concentrations, the limiting and controlling effects may give place to lethal effects which influence the survival of the algae. For example, the concentration of iron, which may at times be a limiting factor in chlorophyll synthesis, may at other times be so low that the phytoplankton cannot manufacture sufficient chlorophyll to survive. At other times, the iron concentration may be so high as to be toxic. The extent to which an algal population grows depends, therefore, upon whether the species in question can survive the conditions in its environment, and upon the degree to which these conditions favour growth.

In the natural environment, the intensity of sunlight, the duration of illumination, and the water temperature vary with climatic and with weather conditions. By climatic conditions we mean here conditions which arise as a consequence of geographic position and the annual rotation of the earth (i.e., the seasonal cycle of changes in solar radiation and in water temperatures). Weather conditions are more irregular, of shorter duration and of more restricted geographic distribution. The climatic conditions may give rise to a comparatively regular cyclic succession of pulses of different algal species. Weather conditions, on the other hand, sometimes alter and obscure the underlying pattern determined by the climate.

The present paper is divided into two parts. The first part deals with the influence of climatic, weather and nutrient conditions on the growth and survival of plankton algae in certain temperate lakes in North America. More particularly, it is concerned with the way in which seasonal changes in water temperatures bring about a seasonal succession of different algal species, and with the way in which weather and nutrient conditions sometimes obscure the cyclic nature of the seasonal distribution of phytoplankton. The second part deals with particular aspects of the climate, weather and nutrient conditions (e.g., light intensity, duration of illumination, temperature, nutrient concentrations, pH, etc.) in terms of the concept of environmental factors (Blackman, 1905; Fry, 1947). In this second part, the data from field investigations are compared with data from laboratory studies of algae in cultures.

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IMPROVING CONDITIONS FOR FISH IN BROWN-WATER BOG LAKES BY ALKALIZATION *

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The object of this study was to discover methods for increasing the productivity of small kettle lakes which have characteristically brown-colored water. Owing to the light-absorbing action of the pigmented solutes and suspensoids of the water, the sun's energy cannot express its optimum effect on the basic fish food supply—plants. Hence, any treatment which would free the water of its brown color and still not be toxic to fish would enhance productivity, since such a treatment would increase the depth of light penetration and therefore the volume of the food-producing (trophogenic) zone. Increased fish production should follow.

James and Birge (1938) and Sauberer and Ruttner (1941) demonstrated that the colored materials of lake water reduced the depth to which the light penetrated. Their results showed also that it was absorbed selectively, especially those wave lengths which were most effective in photosynthesis.

It has been generally observed that seepage water from limed and undrained peat marshes now in use for agriculture is clear, while that from unlimed ones is tea-colored. This observation suggested to us (Hasler and

Einsele, 1948) that lime treatment of acid, brown-water, lakes might likewise clear up the water and therefore increase the depth of the trophogenic zone. Theoretically, if lime were added to lakes the calcium would combine with the humic colloids forming a humate which would flocculate and fall to the bottom. Moreover, alkalization of the water would produce a better medium for bacteria so that suspended organic colloids would be, in part, degraded.

It is well known that acid conditions are unfavorable to decomposition by micro-organisms. We therefore postulated that alkalization through lime treatment might also augment the activities of organic decomposition at the bottom as has been observed in European fish ponds and reviewed by Neess (1948). This action would, theoretically, reduce the rate of accumulation of debris and therefore retard the aging process of the lake and give it additional years of life.

Procedure and Results:

In 1947 a treatment study was initiated on a lake in Langlade County but was given up because of a number of extraneous reasons. However, in 1948 owing to the generous cooperation of Mr. Ben S. McGiveran, Milwaukee, and the International Minerals and Chemical Corporation, Chicago, the project was reestablished on two McGiveran lakes which are in Chippewa County, Wisconsin (T. 32 N.R. 9W).

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They are small kettle lakes with an average depth of 5-6 m. and lie in terminal moraine.

HYDROGRAPHIC DATA
IN ENGLISH AND METRIC UNITS

Lake	Turk		Cather	
	English	Metric	English	Metric
Area	8.8 a.	3.5 ha.	8.4 a.	3.4 ha.
Av. Depth	11.5 ft.	3.5 m.	16.4 ft.	5.0 m.
Max. Depth	19.7 ft.	6.0 m.	32.8 ft.	10.0 m.

Their catchment basins are small, and the soils are poorly drained clay underlaid by hard pan. These edaphic conditions explain the acidity and the paucity of solutes, especially P, N, and Ca (Table 1). The average July air temperature is 68° F.; January, 11.3° F.

Observations on limnological features, including the fishery, were made two years (1948 and 1949) prior to treatment. After removal of the resident fish population by application of derris root, rainbow and brown trout were stocked; a more complete record of the fishery will be published after an examination of the results in the second year of post-treatment.

To alkalize the water before the ice was out in April 1950, finely ground

lime* (calcium and magnesium hydroxide) was used. The chemical was scattered on the ice, but in subsequent additions it was poured over the bow or stern of a rowboat so that the turbulence from an outboard motor churned the powder into the water. Later, a small amount of CaCO₃ was spread near shore. A record of the amounts added and the before and after levels of methyl orange alkalinity, pH, and transparency are given in Table 2. Initial application of lime should be done during the spring or fall circulation (turnover) periods to obtain maximum mixing and hold to a minimum the risk of getting localized lethal concentrations.

By July the water had cleared remarkably in Cather Lake as can be seen from the disk reading in Fig. 1. Because a light meter was not available for pretreatment records a nearby lake, Skow Lake, was chosen for comparison. Limnological and edaphic conditions on this lake are similar to those of Cather and, in addition, transparency readings

* limate = CaO:48.3; MgO = 33.2; H₂O = 16.8. Mfg. by Western Lime and Chemical Company, Milwaukee, Wisconsin.

TABLE 1.—JULY 18, 1949

	Cather		Turk	
	18 July '49	9 Oct. '50	18 July '49	9 Oct. '50
Sol. P.....	—	0.006	—	0.0
Tot. P.....	0.116	0.16	0.120	0.551
SiO ₂	0.266	—	0.320	—
Fe.....	0.112	0.035	0.031	0.05
SO ₄	1.83	1.2	2.25	1.4
Mn.....	0.150	0.076	0.126	0.06
NO ₃ -N.....	0.100	0.09	0.072	0.064
NO ₂ -N.....	0.0026	0.0	0.0016	0.0
NH ₃ -N.....	0.094	0.051	0.166	0.047
T. O. N.....	0.673	0.474	0.266	0.551

Chemical Analysis by courtesy of Prof. G. A. Rohlich, Division of Sanitary Engineering, University of Wisconsin.

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NITROGEN AND PHOSPHORUS CONCENTRATIONS IN FERTILIZED AND UNFERTILIZED FARM PONDS IN CENTRAL MISSOURI¹

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ABSTRACT

The limnology of six typical Missouri farm ponds, where fish growth rates had been determined, was investigated. Particular emphasis was directed toward a measurement of the important nutrient elements, nitrogen and phosphorus, in an effort to evaluate the processes associated with fertilization and establish the nutrient factor or factors most clearly related to fish production for Missouri ponds.

Comparison of the physical and chemical data for these fertilized and unfertilized ponds suggests that the limiting factor in productivity was soluble phosphate. Yearly mean concentrations of phosphate at the surface ranged from 0.016 to 0.028 p.p.m. in the fertilized ponds and from 0.010 to 0.016 p.p.m. in the unfertilized ponds. Daily phosphorus analyses showed good correlation between concentrations of phosphate and plankton production. Each addition of fertilizer was followed by a rapid settling out which resulted in bottom phosphate concentrations which, in one pond, were as much as 10 times as great as the surface concentrations. This phosphate is confined to the bottom by a stable summer stratification in Missouri. Phosphorus added as fertilizer was found to be utilized within one week and on occasion within 24 hours depending on the degree of biological activity.

The occurrence of filamentous algae was correlated with increases in light penetration and soluble phosphate. A pond with filamentous algae showed a much lowered response to fertilization suggesting a removal of nutrients due to absorption by the algal mat.

Nitrogen was not limiting for algal growth in these ponds. Unfertilized ponds showed higher concentration of inorganic nitrogen than did the fertilized ponds. This increased concentration of nitrogen was attributed to the presence of the legume *Lespedeza cuneata* (sericea lespedeza) on the watershed of the unfertilized pond. Quantitative data on nitrogen inflow from the watersheds carrying growths of sericea lespedeza show significantly higher concentrations of inorganic nitrogen in the runoff water.

INTRODUCTION

One of the procedures utilized for the attainment of maximum fish production in farm ponds has been the application of inorganic fertilizers.

¹ Contribution from the Missouri Cooperative Wildlife Research Unit: U.S. Department of the Interior, Fish and Wildlife Service; Wildlife Management Institute; Missouri Conservation Commission; Edward K. Love Foundation; and University of Missouri cooperating. The author wishes to acknowledge the advice of Dr. Robert S. Campbell of the University of Missouri. Special thanks also are due to Paul G. Barnickol and Ralph M. Burress of the Missouri Conservation Commission for critical review of the manuscript.

In soils of low agricultural productivity, water fertilization to increase the growth of pond fish is necessary to compensate for the lack of natural soil fertility. Since poor soils are characteristic of some areas of Missouri, pond fertilization has been included in the farm-pond management program although recommended only where increased production of fish is desirable. The results of fertilization may be unfavorable because of excessive algal development and they are usually difficult to interpret. In an effort to explain these variable results, the limnology of these ponds was investigated with particular emphasis on the measurement of nitrogen and phosphorus which were assumed to be important nutrient elements.

Six experimental ponds were under observation for 14 months. These ponds were considered typical of Missouri farm ponds in that the depth did not exceed 10 feet and the area of each was one-half acre or less. Two of the ponds were fertilized with a 4-12-4 (N-P-K) inorganic commercial fertilizer at the rate of 1,000 pounds per acre per year. Growth of the fish had been determined by Burress² and phytoplankton production in three of the ponds by Proctor.³ A greater growth rate of fish and a higher production of phytoplankton was reported for the fertilized ponds. The present study emphasized: 1. A comparison of nutrient concentrations in fertilized and unfertilized ponds; and 2. A measure of the succession of events which occurred between successive additions of fertilizer.

COMPARISON OF FERTILIZED AND UNFERTILIZED PONDS

Although extensive limnological data were secured, only the material on nitrogen and phosphorus is presented in this paper.

The physical and chemical factors on which data were obtained for the experimental ponds included alkalinity, turbidity, carbon dioxide, mineral content, nitrogen and phosphorus concentration. The only consistent difference between the fertilized and unfertilized ponds was in the amount of phosphorus present.

From the mean yearly phosphorus concentrations in the several ponds (Table 1) it will be seen that the outstanding difference between the fertilized and unfertilized ponds lies in a higher concentration of soluble phosphate on the bottom of the former. Surface concentrations also are higher in the fertilized ponds although the difference is not as great as in the bottom water. Total phosphorus, presumably the best indicator of the potential phosphorus fertility, is found to be higher generally in the fertilized ponds. Since the ratio of the different forms of phosphorus is constantly changing, and since the soluble phosphate is the only form directly available to plankton, a more reliable index to the actual fertility may be found in the percentage concentration of available phosphate

² Burress, Ralph M. 1949. The growth rates of bluegills and largemouth black bass in fertilized and unfertilized ponds in central Missouri. Unpublished Master's dissertation, University of Missouri.

³ Proctor, Vernon W. 1951. A survey of the phytoplankton of three central Missouri farm ponds. Unpublished Master's dissertation, University of Missouri.

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EXPERIMENTAL USE OF FERTILIZER
IN THE PRODUCTION OF
FISH-FOOD ORGANISMS AND FISH

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SUMMARY

Twenty-one ponds at three Michigan fish hatcheries were utilized in the summer of 1946 for experimental work to determine the value of fertilizers in the production of fish. Certain operational difficulties made evaluation of the effects of the fertilizer on the bass-bluegill combinations, and on the minnows difficult, but the general indication was that there was a greater production of these fish in fertilized waters. There was a more clear-cut indication of greater production of crayfish, tadpoles, and other fish in the fertilized waters and it was in the production of fish-food organisms, the lower invertebrates, aquatic insects, and plankton that the greatest difference was noted. The production of invertebrate organisms, as determined by dredge sampling, was 42 percent greater in the fertilized ponds than the non-fertilized ponds, and the production of plankton organisms was 3.3 times as great.

Experimental Use of Fertilizer In the Production of Fish-Food Organisms and Fish

By ROBERT C. BALL*

During the past several years there has been an increasing demand for better fishing in public waters, and along with this there has developed an interest in the possibility of increasing the productivity of natural and artificially impounded waters by the use of fertilizers. This interest has resulted in many requests for information on the advisability and methods of using fertilizer on watered areas to increase fish production.

Much work has been done in southern states (Swingle, 1947; Surber, 1943, 1944) in investigating the effects of the application of fertilizer to fish ponds. Because of the many physical, chemical and climatological differences existing between southern and northern regions, however, it was believed that the recommendations for fertilizing southern ponds would not be applicable to those in Michigan.

To be able to make recommendations concerning methods and materials to be used in such fertilization, it was believed necessary to test the effectiveness of fertilizers on representative Michigan waters, and to determine the most effective rates of application, proper composition of fertilizers, fish species composition, and rates of stocking that can be expected to give desired results.

These broad aims have been only partially considered in this report which is intended as a progress report on certain of the findings.

As a result of the need for this type of information, a co-operative program was set up to investigate certain problems concerning fertilization of Michigan waters. The Institute for Fisheries Research of the Michigan Department of Conservation was to furnish certain materials and personnel, and Michigan State College was to make available facilities necessary to the carrying out of the problem. Three state-owned hatcheries, Wolf Lake, Drayton Plains, and Hastings, all located in southern Michigan, were made available, in part, for experimental work.

*In cooperation with Michigan Institute for Fisheries Research.

As part of the over-all study of fertilization, a fellowship was established by the Institute for Fisheries Research to enable a student at Michigan State College to follow in detail certain of the biological and chemical changes brought about by the application of fertilizer to ponds. This study resolved itself chiefly into a quantitative and qualitative evaluation of plankton from fertilized and unfertilized hatchery ponds and an appraisal of the methods used. The data have been compiled into a Master's thesis (VanDeusen, 1947) and will be published at a later date.

To make possible the collection of adequate data for certain phases of the fertilization project the Institute for Fisheries Research assigned two fisheries technicians for part-time aid on the project. One technician was assigned to Drayton Plains Hatchery and the other to Wolf Lake Hatchery. These men lived full time at the hatchery and worked both on the fertilization project and with the biologist in charge of the minnow-propagation project. As part of their assignment they made collections of fish-food organisms at regular intervals throughout the summer, fertilized the ponds, ran chemical analyses, collected plankton samples, made counts of fry placed in the ponds, and aided in draining the ponds. In many phases of their work they were aided by the hatchery personnel.

Figure 1 is a map of the Wolf Lake State Fish Hatchery, with the ponds used in the fertilization experiments shown in dark lines. These ponds varied considerably in the composition of the bottom-soil types, ranging from a marl-sand mixture to highly organic muck. As well as possible, the ponds were chosen for similarity of bottom type, basin conformation, and water source. The paired ponds utilized were those numbered on the map as follows: 4 (fertilized) and 5; 7 (fertilized) and 11; 9 (fertilized) and 17; and 12 (fertilized) and 10. All of these ponds with the exception of pond 17 received water from the number one spring. The level of the ponds was maintained and no water allowed to overflow the outlet of the fertilized ponds, thus the only loss of water was by evaporation and through the pond basin.

The water source for this hatchery is from three springs and is quite high in carbonate hardness. The methyl orange alkalinity of the three springs is approximately 160 parts per million. Little change was noted in the chemical composition of the water from the time it left the springs until it entered the experimental ponds. All ponds used were small, ranging from 1 acre to 1.8 acres, and having a maximum depth of 6 feet and an average depth of 2½ feet.

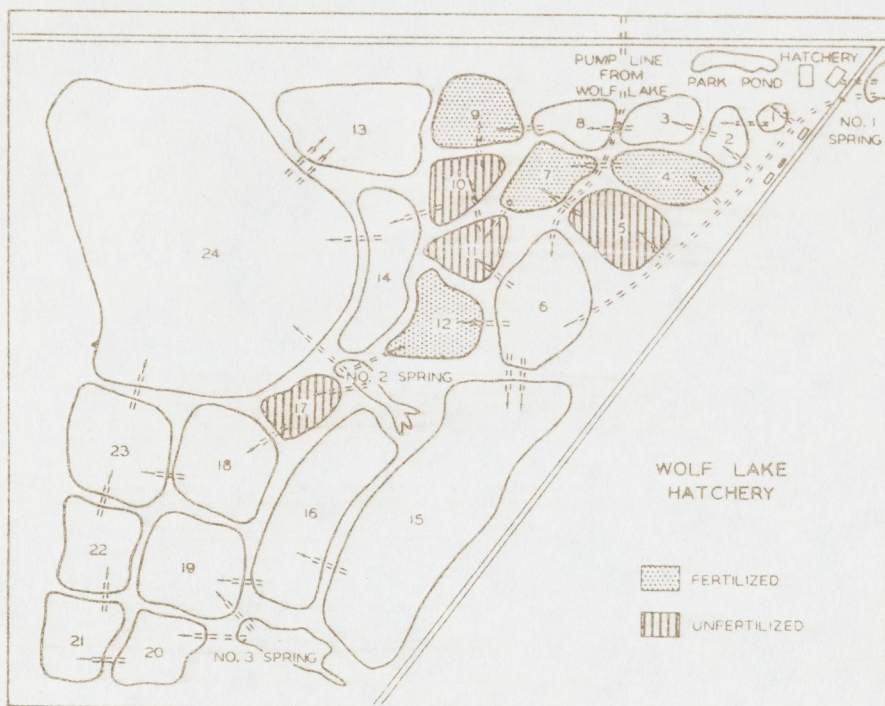


Fig. 1. Wolf Lake Hatchery.

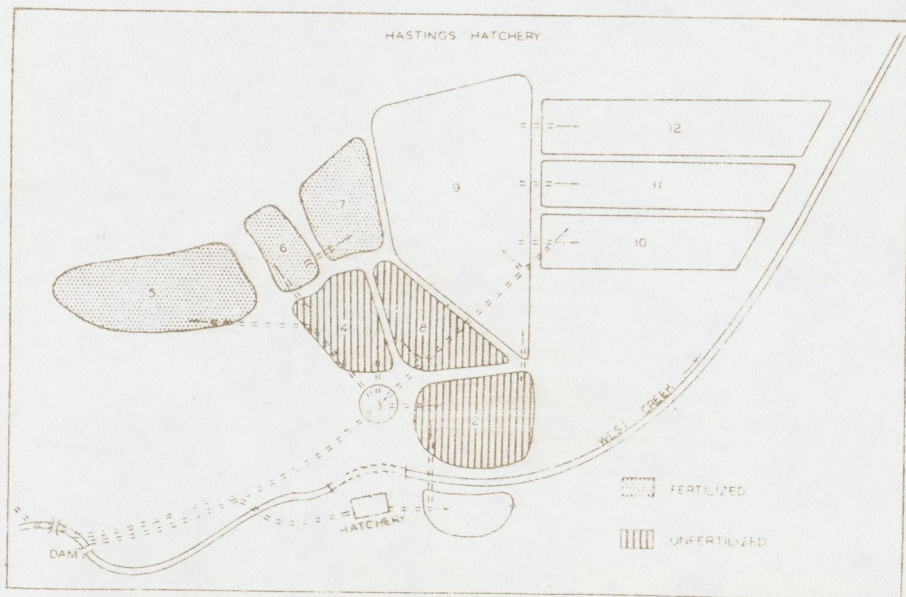


Fig. 2. Hastings State Fish Hatchery.

Figure 2 shows the arrangement of the ponds at the Hastings Hatchery and location of the ponds used in the fertilization experiments. These ponds were quite similar in size and depth to the ponds at Wolf Lake. The water supply is from West Creek, a small stream that supports trout in some sections. The ponds were maintained at a constant level throughout the summer with only enough water flowing in to replace loss through the pond bottom and by evaporation. The methyl orange alkalinity varied slightly during the summer and was approximately 215 parts per million.

The ponds were paired, one receiving fertilizer and the other serving as a control, and each of the pair stocked with fish at the same rate. Pond 5 (fertilized) and 12 were paired, as were pond 6 (fertilized) and 2, 7 (fertilized) and 11, and 8 (fertilized) and 10.

Figure 3 is the plan of the Drayton Plains Hatchery, showing the ponds used in the fertilization experiments. The variation of pond bottom types is greater here than at the other two hatcheries, the ponds having a bottom soil that varied considerably, with much of it being a mixture of sand and marl which does not support dense beds of vegetation such as are present in ponds at the other two hatcheries. Ponds 3 (fertilized) and 4 were paired and stocked with chubs. Ponds 8 and 10 were fertilized and stocked with bass and bluegills, with pond 6 (unfertilized) serving as a control.

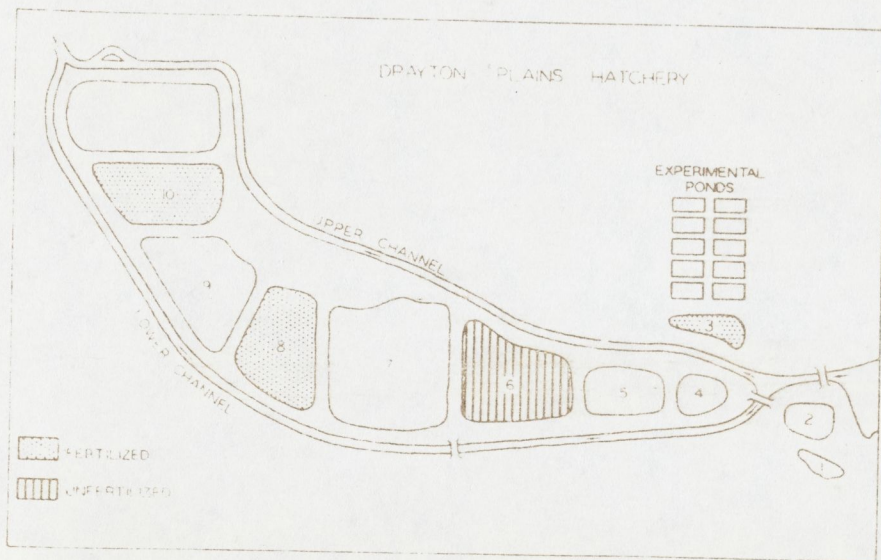


Fig. 3. Drayton Plains Fish Hatchery.

The water supply of this hatchery is from a branch of the Clinton River, a stream flowing through several resort lakes before reaching this hatchery, and is quite variable as to flow and chemical constituents.

ANALYSIS OF FERTILIZER AND METHOD OF APPLICATION

During the 3-month period preceding the start of the field work, greenhouse experiments were conducted under the direction of Dr. Peter I. Tack, of the Section of Zoology, with source waters from the three hatcheries, Wolf Lake, Hastings, and Drayton Plains, to determine the type of fertilizer best suited for these waters. Many fertilizers of different composition were tested and their value determined by the growth of plankton algae in the pots containing the different waters. It was found that a high-nitrogen high-phosphorous fertilizer produced good results (greatest amount of organic matter) in the greenhouse experiments. On the basis of those tests it was determined that a 10-6-4 (N-P₂O₅-K₂O) ratio would be accepted for the first summer's work at these hatcheries. This analysis fertilizer was available from a local distributor.

The commercial fertilizer was applied from a row boat by broadcasting it on the surface of the ponds as evenly as possible. The first application was made on June 18, 1946 and the last on August 26, 1946. The beginning date was later than had been planned, but the scarcity of fertilizer during the spring of 1946 delayed the delivery nearly 2 months. The date of the final application was determined arbitrarily and was approximately 4 weeks prior to the draining of the ponds. It was believed that any application of fertilizer later than this would not be effective in producing any observable change in the fish population before the ponds were drained.

Organic fertilizer in the form of barnyard manure was applied early in the spring to the ponds to be fertilized at both Wolf Lake and Hastings hatcheries, at the rate of 1 ton to each 1½ acres of water surface. A phytoplankton bloom followed this application, and it had been planned to make the first application of inorganic fertilizer before this bloom disappeared, but owing to the delay in obtaining the fertilizer nearly 60 days elapsed before the first application of inorganic fertilizer was made.

To determine the proper interval between applications of fertilizer to the ponds for best results, three application schedules were set up at Wolf Lake Hatchery: once each week, once each 2 weeks, and at

3-week intervals, all applications being at the rate of 33.3 pounds per acre each week. At the conclusion of the summer's work the data on production of plankton showed no advantage in applying the fertilizer at 1- or 2-week intervals over the 3-week period, and the saving of labor in applying the fertilizer at less frequent intervals made its adoption desirable.

Fertilization of the ponds at Drayton Plains and Hastings hatcheries was carried out in much the same manner as at Wolf Lake, except that all ponds were treated at 3-week intervals. The ponds at Hastings Hatchery were treated with barnyard manure prior to the application of inorganic fertilizer. The Drayton Plains ponds received no manure.

PRODUCTION OF MINNOWS

A test of the effectiveness of fertilization in the production of minnows was undertaken in conjunction with the bait-minnow propagation experiment being conducted at the same time by the Institute for Fisheries Research. Two species of minnows, the creek chub, *Semotilus atromaculatus* and the common sucker, *Catostomus commersonii* were used in the experiment.

Ponds at three fish hatcheries were stocked at rates estimated to give the most information concerning the production of these fish for sale as bait. At the hatcheries, ponds were selected in pairs, one to be fertilized and one to serve as a control. These were chosen as nearly as possible for similarity of size, water source, general basin conformation and bottom type. The ponds were fertilized as previously indicated, at the rate of 100 pounds per acre surface area each 3-week interval.

SUCKERS

The suckers were planted as eyed eggs in the ponds at Wolf Lake Hatchery as early in the spring as they were available and were not harvested until the growing season was nearly at an end, so that the production as recorded in Table 1 represents that obtained in nearly the maximum growing season at the latitude of the ponds in Michigan.

From these data only rather broad generalization as to the effect of fertilization can be drawn. The suckers were placed in the ponds in trays in the eyed egg stage, and it was in this stage that the greatest mortality is believed to have taken place. Approximately 7 percent of the eyed sucker eggs that were placed in the fertilized ponds in the spring hatched and lived until the ponds were drained in the

TABLE 1—Data concerning production of suckers in ponds at Wolf Lake Hatchery, 1946

Pond number	Area of pond (acres)	Species planted	Number of fish planted per acre	Number of fish recovered per acre ¹	Percent survival	Pounds of fish recovered per acre ²	Pounds of other fish per acre ³	Pounds of all organisms per acre ³	Average length (inches)	Number per pound	Length when planted inches	Days in pond
4 (fertilized) . .	1.0	Suckers	100,000	8,239	8.2	86.7	0	204	3.3	95	Eyed eggs	144
5 (unfertilized)	1.0	Suckers	100,000	5,769	5.8	96.1	0	183	3.8	60	Eyed eggs	143
7 (fertilized) . .	1.5	Suckers	10,000	2,058	20.0	206.0	45	271	6.7	10	Eyed eggs	148
11 (unfertilized)	1.3	Suckers	10,000	287	2.9	34.1	0	56	7.0	8	Eyed eggs	150
9 (fertilized) . .	1.7	Suckers	50,000	491	1.0	101.0	59	174	8.2	5	Eyed eggs	145
17 (unfertilized)	1.3	Suckers	50,000	5,322	10.6	102.4	0	141	4.0	52	Eyed eggs	149
12 (fertilized) . .	1.8	Suckers	25,000	1,739	6.9	217.4	0	279	7.2	8	Eyed eggs	150
10 (unfertilized)	1.5	Suckers	25,000	24	0.1	0.4	91	267	6.6	6	Eyed eggs	148

¹Species of fish planted in experiment.²Volunteers in pond.³Crayfish, tadpoles, and all fish.

fall. This compares favorably with the survival figures given for Minnesota ponds (Dobie, 1947).

There does appear to be an indication of a greater survival in the fertilized ponds than in the unfertilized ponds, but it should be noted that survival was modified in these experiments to varying and unknown degrees by factors which cannot be quantitatively evaluated, such as loss in the egg stage after being placed in the ponds, predation, and competition by the "volunteer" fish in the ponds, etc. The number and size of unwanted fish in the ponds unquestionably modified the survival of the suckers, and the number of these fish was not constant in the several ponds. That this variability in survival and production may be expected is seen from the experiments in bait-fish production in other states as reported by Dobie, Meehan, and Washburn (1948).

Because of the relatively low survival of suckers it is not probable that the productive capacity of the ponds was reached, unless it was in ponds 5 and 11, both of which were unfertilized and normally quite barren. In these ponds the suckers were observed to be consistently digging small pits in search of food and it was the opinion of the biologist stationed at the hatchery that this digging was only common where the food supply was severely taxed by the number of fish present.

In addition to the suckers, other organisms were present at the time of draining. The bulk of these by weight were tadpoles and crayfish. Their importance as competitors for food in the ponds is not known, but it is quite certain that they were not utilized as food by suckers of the size that were present.

Several other species of fish, including sunfish and darters, were present in the pond. These fish probably were direct competitors for food as well as predators on the small suckers.

The size of the suckers appears to be inversely proportionate to the number present. It was observed that the suckers in the fertilized ponds were of a very uniform size whereas the size of those in the unfertilized ponds was quite variable. This uniformity of size would be quite an advantage in raising bait minnows. Fig. 4 shows graphically the weight relationship of suckers, other organisms, fish-food organisms and plankton.

CHUBS

The fertilization experiment concerning the production of chubs was carried out in eight ponds at the Hastings Hatchery, four fer-

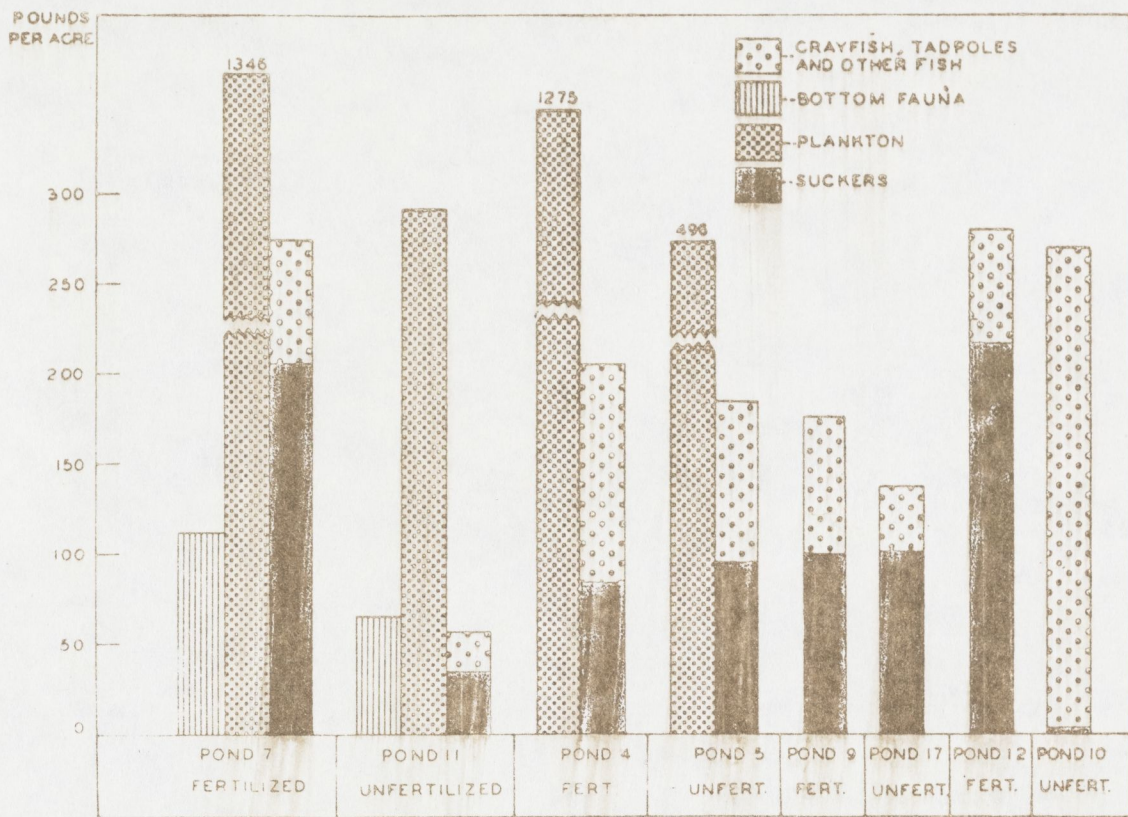


Fig. 4. Production of suckers, bottom fauna, plankton, and other organisms in fertilized and unfertilized ponds at Wolf Lake, 1948.

TABLE 2—Data concerning production of chubs at Hastings Hatchery, 1946

Pond number	Area of pond (acres)	Species planted	Number of fish planted per acre	Number of fish recovered per acre ¹	Percent survival	Pounds of fish recovered per acre ¹	Pounds of other fish per acre ²	Pounds of all organisms per acre ³	Average length (inches)	Number per pound	Length when planted (inches)	Days in pond
5 (fertilized)...	2.1	Chubs	10,000	200	2.0	10.8	96	4.8	18	Sac fry	135
12 (unfertilized)	1.5	Chubs	10,000	145	1.5	4.7	45	4.3	31	Sac fry	135
6 (fertilized)...	.6	Chubs	44,000	6,875	15.6	136.5	352	3.9	50	Sac fry	129
2 (unfertilized)	1.0	Chubs	25,000	4,500	18.0	50.0	250	3.1	90	Sac fry	129
8 (fertilized)...	1.0	Chubs	35,000	1,312	3.8	31.0	160	3.7	43	Sac fry	128
10 (unfertilized)	1.0	Chubs	35,000	2,880	8.2	80.0	122	3.7	36	Sac fry	129
7 (fertilized)...	1.1	Chubs	25,000	308	1.2	8.1	70	4.4	38	Sac fry	135
11 (unfertilized)	1.3	Chubs	25,000	67	.3	1.8	53	4.2	32	Sac fry	135

¹Species of fish planted in experiment.²Volunteers in pond.³Crayfish, tadpoles, and all fish.

tilized and four controls, and one pair of ponds at the Drayton Plains Hatchery. Each pair of ponds was stocked at the same rate with sac fry, which had been hatched in hatchery jars and held in troughs until the yolk sac was nearly absorbed.

Table 2 shows the data pertaining to the production of chubs at the Hastings Hatchery. The same factors affected the survival of these fry as were considered for the Wolf Lake experiment with suckers and, in general, the same tentative conclusions as to the effect of fertilizer apply. The survival of chubs at Hastings was 6.3 percent. Variation of the rate of survival in the several ponds was large. Here, too, the factors affecting survival were not closely, if at all, tied in with fertilization and no evaluation of the effect of fertilization on survival can be made. In the draining of these ponds, no effort was made to separate the volunteer fish from the other organisms (crayfish and tadpoles) and the weight of these is shown in the table under the heading "all organisms". The fertilized ponds produced, without exception, a greater total weight of organism than did the unfertilized ponds, in most cases considerably greater. The weight relationship of the chubs in fertilized and unfertilized ponds at the Hastings Hatchery, and this relationship to other organisms is shown in Fig. 5. Two small ponds at the Drayton Plains Hatchery were stocked with chub fry and data on the production of these two ponds are shown in Table 3. These fish had a somewhat shorter growing season than those at Hastings and the production in pounds per acre was considerably less, notwithstanding the greater survival. A comparison of the production of these two ponds is shown graphically in Fig. 6.

PRODUCTION OF BASS AND BLUEGILLS

To be better able to make recommendations concerning desirable species combinations and the rates at which different components of the population should be stocked, the workers stocked largemouth bass and bluegills at different rates in ponds at Drayton Plains Hatchery. The stocking rates, rate of recovery, and the size of fish recovered in the three experimental ponds are shown in Table 3. From this table it can be seen the survival rate of the bass, which were planted as advanced fry of about one inch in length, was high, whereas the survival of the bluegills, which were planted as golden fry, was quite low. The survival and production of both the bass and bluegills was influenced by the presence of other fish in ponds 6 and 10. The Brook Stickleback (*Eucalia inconstans*) was the most important "volunteer" fish,

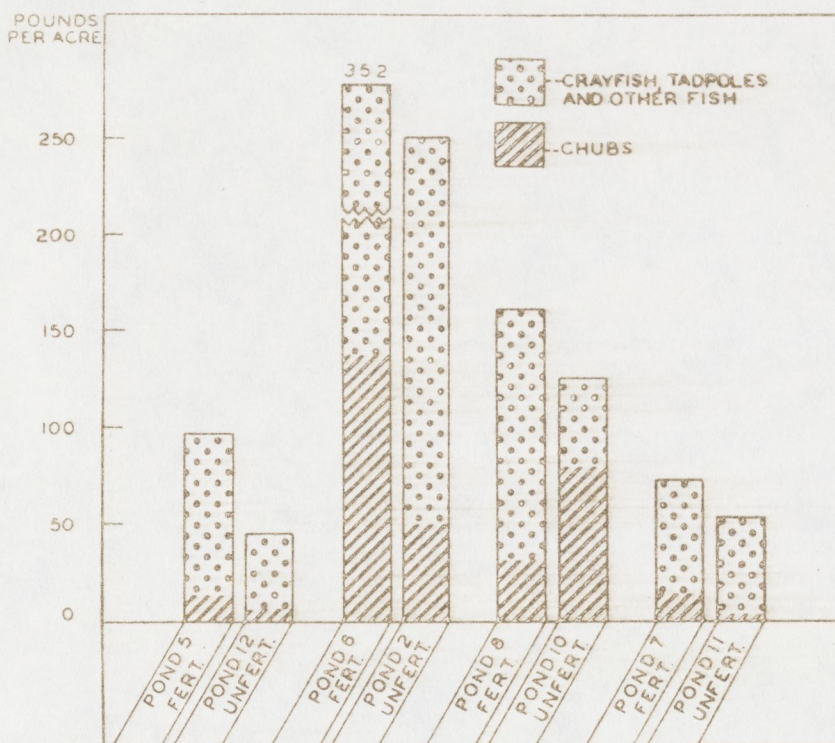


Fig. 5. Production of chubs and other organisms in fertilized and unfertilized ponds at Hastings Hatchery, 1946.

there being approximately 113,000 in pond 6 at the time it was drained. It is extremely difficult to keep the ponds free from this fish if it occurs in the water supply and it is both a competitor of and predator on the young of other fish.

From these experiments it can be seen that stocking of bluegill fry was not satisfactory under the conditions existing at the time. The difficulties a pond owner would have in obtaining and positively identifying bluegill fry, and of predicting survival to adult size, which must be done to assure a proper balance in the pond, make it desirable that the bluegills be stocked as adults and the bass as fingerlings or adults.

The actual survival of the young bass and bluegills was not accurately established in pond 6, as indicated by the taking of more small bass at the end of the growing period than were planted as advanced fry. This was due to the water source being well supplied with fry of the same size as those planted, and the screening between the water

TABLE 3—Data on production of largemouth bass, bluegills, and chubs, and the survival of young fish in ponds at Drayton Plains Hatchery, 1946

Pond number	Area of pond (acres)	Species planted	Number of fish planted per acre	Number of fish recovered per acre ¹	Percent survival	Pounds of fish recovered per acre ²	Pounds of other fish per acre ¹	Pounds of all organisms per acre ²	Average length (inches)	Number per pound	Length when planted (inches)	Days in pond
6 (unfertilized).	3.7	Bass	200	236	118	15.1	30.6	153.5	4.9	16	1	67
		Bluegills	3,000	300	10	1.7			2.5	200	Fry	
8 (fertilized)...	3.7	Bass	270	220	79	7.1	0	30.0	4.3	32	1	71
		Bluegills	4,000	220	18.2	1.0			1.9	220	Fry	
10 (fertilized)...	7.1	Bass	1,000	720	71	25.8	3.5	247.5	4.3	27	1	73
		Bluegills	15,000	930	6.3	5.5			2.1	170	Fry	
3 (fertilized)...	.46	Chubs	38,500	19,908	51	102.6	0	246	2.5	194	Fry	114
4 (unfertilized).	.48	Chubs	32,000	23,380	73	112.5	0	133.3	2.5	208	Fry	114

¹Species of fish planted in experiment.²Volunteers in pond.³Crayfish, tadpoles, and all fish.

source and this pond not adequate to keep out the smallest fish. It does not seem that the carrying capacity of any of the ponds was approached in the number and weight of bass and bluegills produced. Figure 6 shows the relationship of bass and bluegills to other organisms and to the average standing crop of invertebrate fish-food organisms.

The data on the production in the two ponds at Drayton Plains Hatchery that were stocked with chubs, shown in Fig. 6, indicate a considerably greater production of total organisms in the fertilized pond than in the unfertilized pond, but the production of chubs was lower in the fertilized pond.

The somewhat lower production of chubs may have been due to the competition of the other organisms for food. Very little can be concluded as to the value of fertilization in the production of bass, bluegills, and chubs from this experiment, but there is experimental

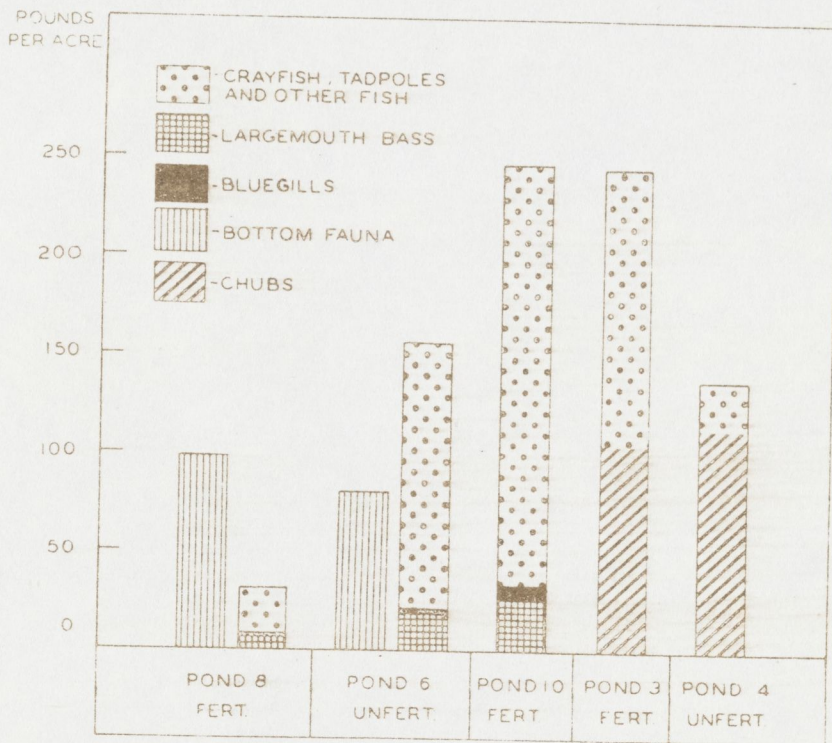


Fig. 6. Production of fish, bottom fauna, and other organisms in fertilized and unfertilized ponds at Drayton Plains Hatchery, 1946.

evidence that the addition of fertilizer to a pond does produce greater total weight of all organisms, (fish, crayfish, tadpoles, invertebrates).

FISH-FOOD ORGANISMS

To evaluate further the effects of fertilizer and more thoroughly understand the action of fertilizer on the food chain of the fish, a program of sampling the invertebrate fish-food organisms was undertaken at both the Wolf Lake and Drayton Plains hatcheries. These samples were collected at regular intervals from each of a pair of ponds, one fertilized and one unfertilized, by the biologist stationed at each hatchery. The sampling was by means of either a Peterson or Ekman dredge, depending upon the bottom type.

The results of collections made in ponds 6 and 8 at Drayton Plains are tabulated in tables 4 and 5. The organisms shown in the tables have been tabulated by percentage of total volume and percentage

TABLE 4—*Invertebrate fauna collected by bottom sampling, 1946, Drayton Plains Hatchery Pond No. 6 (unfertilized)*

Collection period.....	June		July		August		Totals	Percent of total
	16-30	1-15	16-31	1-15	16-31			
No. of samples.....	6	17	13	10	10	56		
Total area (sq. ft.).....	4.97	14.07	10.76	8.28	8.28	46.37		
Total no. of org.....	103	813	921	288	204	2329		
No. org. per sq. ft.....	21	58	86	35	25	(ave) 50		
Total vol. organisms.....	5.10	13.25	8.80	8.20	4.40	39.75		
Vol. org. per sq. ft.....	1.03	0.94	0.82	0.99	0.53	(ave) 0.86		
Chironomidae.....	No. 38 Vol. (cc) 0.25	621 1.50	668 2.00	130 0.55	84 0.50	1541 4.80	66.1 12.1	
Anisoptera.....	No. 20 Vol. 1.20	35 4.45	26 2.95	7 0.25	19 0.60	107 9.45	4.6 23.8	
Zygoptera.....	No. Vol.		7 0.15	6 0.20	6 0.25	19 0.60	0.8 1.5	
Ephemera.....	No. 4 Vol. 0.15	100 0.70	149 0.65	94 0.55	67 0.50	415 2.55	17.8 6.4	
Trichoptera.....	No. 1 Vol. 0.05		24 0.50	7 0.25	6 0.20	38 1.00	1.6 2.5	
Coleoptera.....	No. 12 Vol. 0.20	10 0.30	23 0.50	16 0.40	10 0.30	72 1.70	3.1 4.3	
Hemiptera.....	No. Vol.	4 0.20	4 0.15			8 0.35		
Annelida.....	No. Vol. 2.85	6.00	1.90	5.95	2.05	18.75	46.5	
Amphipoda.....	No. 16 Vol. 0.35	2 0.10				18 0.45	0.8 1.1	

TABLE 5—Invertebrate fauna collected by bottom sampling, 1946, Drayton Plains Hatchery Pond No. 8 (fertilized)

Collection period	June		July		August		Totals	Percent of total
	16-30	1-15	16-31	1-15	16-31			
No. of samples	7	15	14	8	10		54	
Total area (sq. ft.)	5.80	12.42	11.60	6.62	8.28		44.71	
Total no. of org.	125	1337	1350	603	657		4072	
No. org. per sq. ft.	22	108	116	91	79		(ave.) 91	
Total vol. organisms	4.15	9.00	13.15	9.60	10.45		46.35	
Vol. org. per sq. ft.	0.72	0.81	1.13	1.45	1.25		(ave.) 1.04	
Chironomidae	No. Vol. (cc) ..	84 0.45	1002 4.00	996 4.65	398 0.65	425 1.80	2005 10.55	71.3 22.8
Anisoptera	No. Vol.	30 1.35	11 1.60	11 0.55	13 0.80	14 0.65	79 4.95	1.9 10.7
Zygoptera	No. Vol.		1 0.05	23 0.40	34 0.35	36 0.40	94 1.20	2.3 2.6
Ephemera	No. Vol.		289 1.30	285 1.45	130 0.75	161 1.15	865 4.65	21.24 10.0
Trichoptera	No. Vol.	3 0.10			1 0.05		4 0.15	
Coleoptera	No. Vol.		20 0.50	17 0.35	7 0.15	6 0.20	50 1.20	1.2 2.6
Hemiptera	No. Vol.		1 0.05		1 0.05		2 0.10	
Lepidoptera	No. Vol.		2 0.05				2 0.05	
Annelida	No. Vol.		2.25 2.90		5.70 6.70	7.40	23.30	50.3

of total number. From these data it can be seen that the Annelida constitute a large percentage of the total volume in all ponds, ranging from approximately 33 percent to more than 50 percent of the total. Included under the heading "Annelida" were the large aquatic earthworms which were common in all ponds at Wolf Lake Hatchery, the smaller tubificids, and the leeches. The annelids were not considered of much importance as fish food in these ponds as the large earthworms were deep enough in the pond bottom material to be unavailable to the fish. The tubificids were few in number, and the leeches, which were volumetrically important in the samples from Drayton Plains, were nearly all very large individuals and, thus, not available as food for the young-of-the-year fish.

The results of the collections from the two ponds at Drayton Plains are shown graphically in Fig. 8. From the chart, which was plotted from the data on the daily collections, it can be seen that the volume

of bottom-dwelling organisms was greater in pond 8, the unfertilized pond, at the beginning of the fertilization period. This is believed to be a true representation of the productivity of the ponds, which, although chosen as being quite similar in size and depth, proved quite different biologically. The bottom material in pond 6 was richer in organic matter and was without the sand-marl deposits which made areas of the bottom of pond 8 quite barren.

The curves representing the volumes of organisms per unit area of the paired ponds show the low point of the collection period to be early in summer, a condition found in a natural lake in the same general area (Ball, 1948) and one which corresponds with the period of

TABLE 6—Invertebrate fauna collected by dredge sampling, 1946, Wolf Lake Hatchery Pond No. 7 (fertilized)

Collection period.....	June	July		Aug.		Sept.	Totals	Percent of total
	16-30	1-15	16-31	1-15	16-31	1-15		
No. of samples.....	10	20	13	7	18	16	84
Total area (sq. ft.).....	8.28	8.28	5.38	2.90	7.45	6.63	38.92
Total no. of org.....	385	136	245	278	288	145	1479
No. org. per sq. ft.....	47	16	45	96	39	22	(ave.) 38
Total vol. organisms.....	12.90	5.05	4.65	5.50	9.70	8.20	46.00
Vol. org. per sq. ft.....	1.55	0.61	0.86	1.90	1.30	1.24	(ave.) 1.18
Chironomidae...	No. 195 Vol. (cc).... 4.05	54 1.05	89 1.00	215 2.40	264 3.25	132 1.35	949 13.10	64.1 28.5
Anisoptera.....	No. 1 Vol. 0.05	3 1.35	1 0.05	3 0.75	2 0.10	10 2.30	0.7 5.0
Zygoptera.....	No. Vol.	3 0.10	1 0.05	1 0.05	5 0.20
Ephemera.....	No. 106 Vol. 0.85	38 0.55	130 0.85	24 0.25	6 0.10	309 2.60	20.9 5.6
Trichoptera.....	No. 7 Vol. 25	7 0.25
Coleoptera.....	No. 15 Vol. 0.25	5 0.25	1 0.05	21 0.55	1.4 1.2
Hemiptera.....	No. 5 Vol. 0.20	1 0.05	6 0.25
Annelida.....	No. Vol. 6.20	1.15	2.30	1.70	5.90	6.40	23.65	50.8
Nematoda.....	No. Vol.	5 0.15	6 0.10	4 0.15	5 0.15	20 0.75	1.4 1.2
Amphipoda.....	No. 16 Vol. 0.20	14 0.15	19 0.25	28 0.20	13 0.15	6 0.20	96 1.15	6.5 2.5
Arachnida.....	No. 3 Vol. 0.10	1 0.05	4 0.15
Snails.....	No. 23 Vol. 0.50	15 0.30	1 0.05	1 0.05	40 0.90	2.7 2.0

peak emergence in lakes in this latitude. Following this low point the production in both ponds took an upward swing and the standing crops of fish-food organisms were about equal in the third week of July, but from this time on the fertilized pond showed an increase in the volume of organisms per unit area and the unfertilized pond did not.

Data concerning the collections of fish-food organisms in fertilized and unfertilized ponds at Wolf Lake are tabulated in Tables 6 and 7.

TABLE 7—*Invertebrate fauna collected by dredge sampling, 1946, Wolfe Lake Hatchery Pond No. 11 (unfertilized)*

Collection period.....	June	July		Aug.		Sept.	Totals	Percent of total	
	16-30	1-15	16-31	1-15	16-31	1-15			
No. of samples.....	10	20	14	10	28	2	84	
Total area (sq. ft.).....	7.28	8.28	5.80	4.14	11.59	.83	38.98	
Total no. of org.....	254	221	247	128	280	15	1145	
No. org. per sq. ft.....	35	27	43	31	24	18	(ave.) 29	
Total vol. organisms.....	9.00	4.15	4.45	2.10	7.25	.25	27.20	
Vol. org. per sq. ft.....	1.24	0.50	0.77	0.51	0.63	.63	(ave.) 0.70	
Chironomidae.....	No..... Vol. (cc).....	144 0.95	113 0.95	46 0.60	57 0.60	179 1.60	13 .10	552 4.80	48.2 17.6
Other diptera.....	No..... Vol.....	3 0.10	2 0.10		1 0.05			6 0.25	0.9
Anisoptera.....	No..... Vol.....	24 0.75	3 0.15	8 0.40	3 0.10	4 0.40		42 1.80	3.7 6.6
Zygoptera.....	No..... Vol.....		1 0.05	7 0.20	1 0.05	16 0.50		25 0.80	2.2 2.9
Ephemeroidea.....	No..... Vol.....	4 0.15	61 0.60	106 0.75	22 0.40	29 1.15		222 3.05	19.4 11.2
Trichoptera.....	No..... Vol.....	6 0.15	2 0.05	1 0.05		1 0.05		10 0.30	0.9 1.1
Coleoptera.....	No..... Vol.....	1 0.05	1 0.05	1 0.05		1 0.05		10 0.20	0.9
Hemiptera.....	No..... Vol.....			2 0.05			2 0.05	4 0.10	
Aphididae.....	No..... Vol.....			1 0.05	3 0.10			4 0.15	
Annelida.....	No..... Vol.....			1 1.60	0.40	2.60	0.10	3.90	32.7
Amphipoda.....	No..... Vol.....	60 0.65	30 0.45	69 0.60	39 0.35	44 0.75		242 2.80	21.1 10.3
Crayfish.....	No..... Vol.....	3 2.80	2 0.70					5 3.50	12.9
Arachnida.....	No..... Vol.....				1 0.05			1 0.05	
Snails.....	No..... Vol.....	3 0.10	4 0.15	2 0.10		3 0.15		12 0.50	1.0 1.8

These data are shown graphically in Fig. 8. This chart shows about the same condition as was noted in collections from the Drayton Plains ponds; that is, the high point for the season during which collections were made was early in the period, followed by a rapid falling off of the volume during mid-July. The recovery of volume of organisms in the fertilized pond following this period was quite rapid but the unfertilized pond did not show this rapid recovery.

About the middle of July the fish in the ponds reached a size at which they began feeding on the macroscopic invertebrates, and as is seen in both Figs. 7 and 8 the invertebrates in the fertilized ponds were able to maintain themselves or increased in spite of the increasing size of the fish population with the accompanying demand on the food supply, whereas the total volume of invertebrates in the untreated ponds declined as the fish population increased.

This increase in volume and maintenance of a greater volume of fish food in the fertilized pond is even more significant in view of the

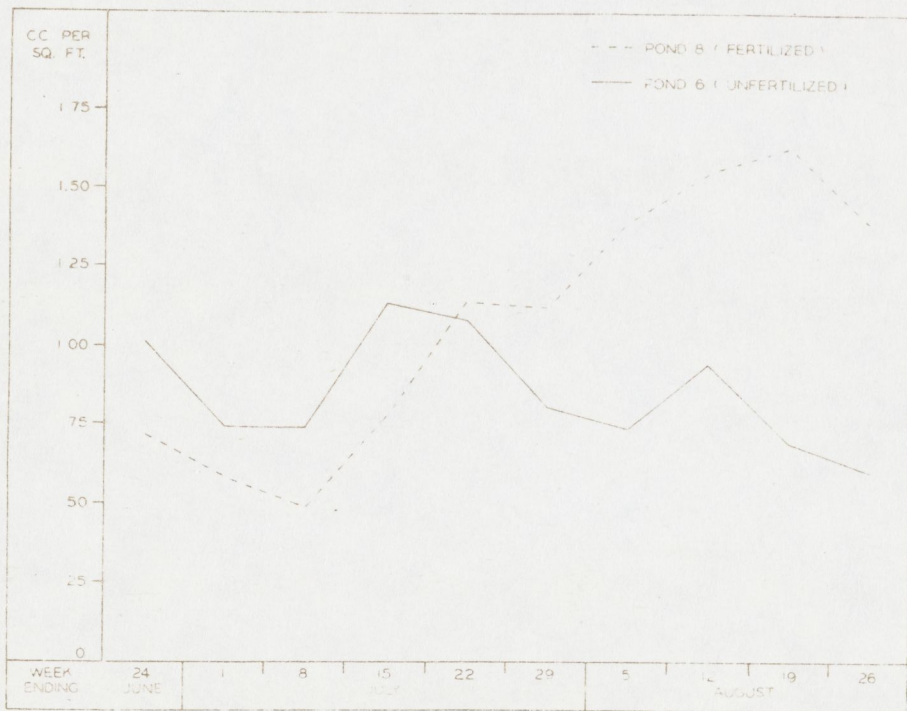


Fig. 7. Volume per unit area of invertebrate fish-food organisms in fertilized and unfertilized ponds at Drayton Plains Hatchery, 1946.

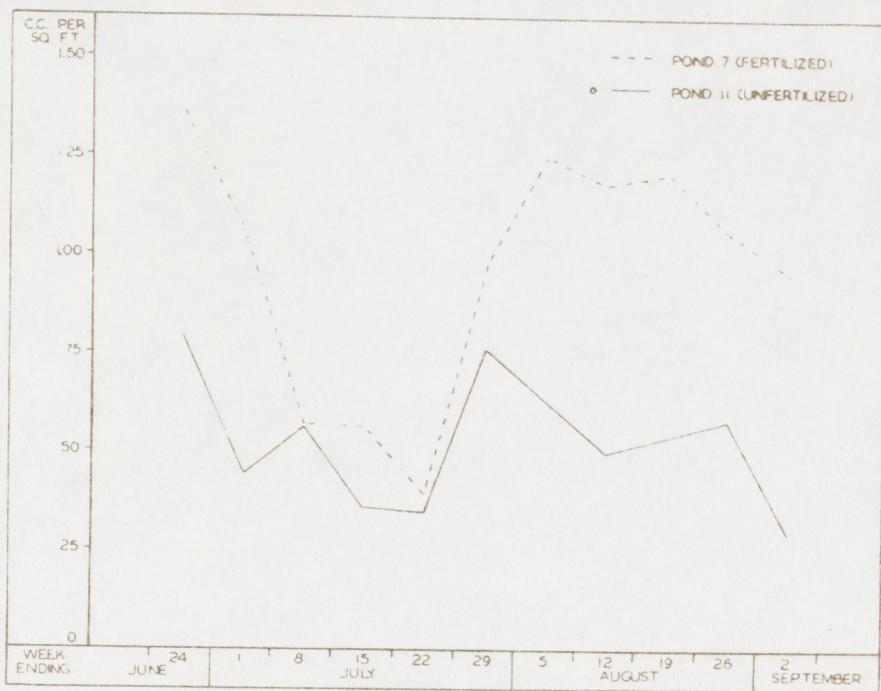


Fig. 8. Production of invertebrate fish-food organisms in fertilized and unfertilized ponds at Wolf Lake, 1946.

expressed belief by the hatchery superintendent that, of the paired ponds at Drayton Plains, the unfertilized pond had been, in past years, more productive than the fertilized pond.

In Table 8 are presented the data showing the percentage composition by volume, of invertebrates collected from the ponds.

TABLE 8—Percent by volume composition of important invertebrates in dredge samples from fertilized and unfertilized ponds¹

Species	Drayton Plains		Wolf Lake	
	Fertilized	Unfertilized	Fertilized	Unfertilized
Midges	22.8	12.0	28.5	17.6
Dragonflies	13.3	25.3	5.4	9.5
Mayflies	10.0	6.4	5.7	11.2
Beetles	2.6	4.3	1.2	0.7
Annelida	50.3	46.5	50.8	32.7

¹Those constituting more than 1 percent of the total volume.

Observations on paired ponds indicate that of the aquatic insects it often is the midge population that increases first and most rapidly in ponds where fertilizer is applied. The midges, having more than one generation per year, respond rapidly to a favorable change in the environment such as presumably is brought about by the fertilizer.

The difference of the average standing crops of macroscopic invertebrates as determined by sampling in the four ponds is shown in Table 9. From this table it can be seen that the potential fish food, as measured in pounds per acre, is considerably greater in the fertilized ponds, as much as 68 percent in the paired ponds at Wolf Lake and 21 percent in the ponds at Drayton Plains Hatchery. It is believed that this appreciably greater standing crop of fish-food organisms in the fertilized ponds can be considered as a direct result of fertilization.

COMPARISON OF SIZE OF INDIVIDUAL ORGANISMS IN FERTILIZED AND UNFERTILIZED PONDS

In the belief that the effects of fertilization might be reflected in the size (volume) of the individual organisms, the average volume of individual organisms was determined for several of the invertebrates in both fertilized and non-fertilized ponds. From this comparison came an indication that the individual chironomids are larger in the fertilized ponds. This difference in size was not so pronounced, or not evident at all, in other forms considered. The specific identification of species involved was not determined and it may be that had such been

TABLE 9—Volume of fish-food organisms collected in ponds at Wolf Lake and Drayton Plains hatcheries, 1946

Pond number	Average number per square foot	Average volume per square foot c.c.	Pounds per acre
<i>Wolf Lake</i>			
7 (fertilized)	38	1.18	113.3
11 (unfertilized)	29	.70	87.2
<i>Drayton Plains</i>			
8 (fertilized)	91	1.04	99.9
6 (unfertilized)	50	.86	82.6

done the differences in size would not have been valid but it is indicated that the general tendency is toward larger individual size in the fertilized ponds.

PLANKTON

Plankton samples throughout the period of fertilization were taken at weekly intervals from two fertilized and two non-fertilized ponds at the Wolf Lake Hatchery. These collections were evaluated in several ways (VanDeusen, ms.) but for purposes of this report only the counts, which were made by the Sedgwick-Rafter method, and the volumetric estimates, which were made by precipitating out the plankton organisms with a mercuric chloride solution and measuring in a graduated centrifuge tube are considered. In computing the total volume of plankton, zooplankton and phytoplankton organisms were considered together but this lumping of the two groups changed the total volume very little as there were few zooplankters in the ponds during most of the summer. It is assumed that the volume of phytoplankton is a better criterion of production of organic matter than are the numerical counts.

A tabulation of these collections by number of organisms is shown in Table 10 and by volume of organisms in Table 11. From these tables it is seen that the number of plankters per unit volume of water is far greater throughout the entire period considered in fertilized

TABLE 10—Number of plankton organisms per liter in fertilized and unfertilized ponds at Wolf Lake Hatchery, 1946*

Date	Pond 4 (fertilized)	Pond 5 (unfertilized)	Pond 7 (fertilized)	Pond 11 (unfertilized)
July 1	4,317,000	1,014,000	376,000	376,000
8	4,775,000	654,000	458,000	378,000
15	8,062,000	392,500	441,500	327,000
22	8,880,000	441,500	212,500	474,500
29	18,430,500	131,000	310,500	245,500
Aug. 5	10,155,500	310,500	2,191,500	147,000
12	9,485,000	327,000	2,534,500	294,500
19	8,536,500	294,500	8,373,000	245,500
26	8,749,500	327,000	13,573,500	376,000
Sept. 3	13,606,500	474,500	22,748,500	359,500
9	20,884,000	507,000	9,484,500	425,000
Total	115,881,500	4,873,500	60,705,000	3,646,500
Average	10,534,682	443,046	5,518,637	331,500

*Data from VanDeusen (ms).

TABLE 11—Weight of plankton organisms in grams per liter in fertilized and unfertilized ponds at Wolf Lake Hatchery, 1946*

Date	Pond 4 (fertilized)	Pond 5 (control)	Pond 7 (fertilized)	Pond 11 (control)
July 1.....	0.10 g/l	0.15 g/l	0.27 g/l	0.03 g/l
8.....	.13	.12	.11	.04
15.....	.23	.07	.06	.05
22.....	.24	.13	.05	.05
29.....	.17	.05	.07	.05
Aug. 5.....	.18	.03	.15	.03
13.....	.22	.07	.15	.03
19.....	.18	.03	.21	.05
26.....	.17	.03	.45	.04
Sept. 2.....	.18	.02	.28	.05
9.....	.18	.06	.33	.05
Average.....	0.18	0.07	0.10	0.04
Pounds per acre average depth.....	1275	496	1346	283
Pounds per acre foot.....	510	168	538	113

*Data modified from VanDeusen (ms).

than in the non-fertilized ponds. The volume of plankton organisms per unit was also higher in fertilized ponds, averaging 510 pounds per acre foot for the two fertilized ponds as compared with an average of 156 pounds per acre foot in the two untreated ponds.

Table 12 summarizes the weights of fish, tadpoles and crayfish, invertebrate fish-food organisms, and plankton produced in fertilized and unfertilized ponds during a single growing season. These data are averages of all ponds utilized in the fertilization studies at the three state fish hatcheries where the studies were carried out and as a result show the over-all picture without pointing out the individual variations that did occur. From the other data presented in this paper it is evident that not in every case will the fertilized pond produce greater weights of organisms per unit area than a similar non-fertilized

TABLE 12—Summary of production in pounds per acre of fish and other organisms in fertilized and non-fertilized ponds at three state fish hatcheries, 1946

	Large-mouth Bass	Chubs	Bluegills	Suckers	Bottom Organisms	Tadpoles	Plankton
Fertilized ponds..	16.5	75	3.3	153	106	113	524*
Unfertilized ponds	15.1	74	1.7	58	75	76	156*

*Weight per acre foot.

one. It is also evident from this work that ponds which have been chosen for similarity of physical, chemical, and biological detail will often react quite differently to the stimulus of an application of fertilizer. These differences in similar ponds have been observed by other workers who have attempted to use untreated ponds as controls for fertilized ponds, (Swingle, 1947) however, the data presented in the table do show a uniformity in that, in every case, the average production of fertilized ponds was greater than the unfertilized ponds.

While there may not be enough data to justify a generalization, it does appear that the closer the feeding habits of the fish concerned are to the base of the food chain the more the effects of fertilizer are reflected in total weight of fish produced. The effect of fertilizer upon the lower vertebrates, invertebrates, and plankton organisms is much more pronounced than on the fish.

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On the Theory of Adding Nutrients to Lakes with the Object of Increasing Trout Production

by

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The object of tampering with the economy of a lake is to increase the fish crop. There are few experiments on record showing clearly what added nutrients will do in this direction. There are however, records for a large series of lakes, principally European, where inadvertent fertilization has occurred as a result of domestic sewage or agricultural drainage (Hasler 1947).

A noteworthy example is Lake Zurich, Switzerland, a lake composed of two basins separated by a narrow passage. Less than 100 years ago both basins were clear and supported a commercial crop of trout and whitefish. For the last 50 years or more, one basin has received urban drainage from communities numbering 110,000 people. One result has been the development of algal scums, which made the lake unattractive. Moreover decomposition of the added organic matter produced a deficiency of oxygen in the deeper water so that trout and one species of whitefish disappeared altogether; two others are rarely seen any more. Other species, largely coarse fish, have replaced them.

The other basin, which receives no urban drainage, has changed little. Hasler assembled records for 37 lakes which had been unintentionally enriched, and whose history followed within a few decades, that of Lake Zurich. In all cases the results were not in the best interest of ideal lake use by man. Continuous nutrient drainage into a lake will undoubtedly produce enrichment, but if coarse fish are present they are likely to be favoured at the expense of trout, and there will probably be other unwanted results.

Intentional Enrichment of Lakes

Turning now from unintentional to intentional enrichment, two important differences should be noted. First, the amounts of nutrient added will be very much reduced, for obvious economic reasons. Second, the addition will not be continuous, but will occur when fertilizer is spread over the lake once or twice a year. The question for us then, is whether one addition or an occasional addition of fertilizer can improve trout production. It may be said at once that there is no experiment known to the writer, in which permanent improvement in trout fishing has been demonstrated, following such fertilization.

The nutrients which come to mind are those known to be useful in agriculture, namely nitrogen, potassium and phosphorus. When these substances are added they always disappear rapidly from the water, so that some 90 per cent is gone within a month or less. This has often been taken as evidence of rapid utilization by the animals and plants in the lake, and it has been thought to prove that the added material was acting as a nutrient.

Bottom Fauna of a Shallow Eutrophic Lake, Lizard Lake, Pocahontas County, Iowa¹

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The State of Iowa is carrying on a dredging program in an attempt to rehabilitate many of the lakes in the northern part of the state. Most of these lakes are of glacial origin and are in the later stages of succession. They are of little value for boating and swimming because of the shallow depth and heavy growths of aquatic vegetation. The fish populations in many of them cannot be maintained because of their vulnerability to winter kill. By means of dredging, the life of these lakes is prolonged and sufficient depth is provided to support a fish population throughout the year. The increased depth and decrease in aquatic vegetation makes them more suitable as recreational areas. Conditions in these lakes are radically altered as a result of dredging and it is desirable to know what effect this has on the biological productivity. The bottom organisms are directly affected by dredging and it is believed that they can be used as an index to measure any changes in the productivity of these lakes.

Lizard Lake was selected for a bottom fauna study because it will be dredged in the near future. This paper deals with the data gathered from Lizard Lake in the summer of 1951, before dredging of the lake, and will provide a basis for comparing the productivity in terms of bottom fauna after the lake has been dredged. Several sampling techniques were used to determine which would give the best results in different types of habitat.

Lizard Lake, located in Lake Township, Pocahontas County, Iowa, has a surface area of approximately 268 acres (fig. 1). The maximum depth found in July, 1951, was 5 feet and much of the lake was between 4 and 5 feet deep. There are no docks or cottages around the lake and the surrounding land is devoted entirely to agriculture. Most of the land in the immediate vicinity of the shoreline is wooded or open pasture. The main inlet flowing into the shallow bay at the southwest corner of the lake provided water throughout the summer of 1951. The outlet is at the north end of the lake and drains into the west fork of Lizard Creek and thence to the west fork of the Des Moines River.

Chemical and temperature readings indicated very little stratification from top to bottom during most of the summer. By the middle of August most of the surface of the central part of the lake was covered with a dense growth of sago pondweed, *Potamogeton pectinatus*. Methyl orange alkalinity ranged from 180 to 230 parts per million during the summer. Turbidity was almost entirely due to silt suspended in the water after periods of high wind. On calm days the Ekman sampler could be seen on the bottom at a depth of 4 feet.

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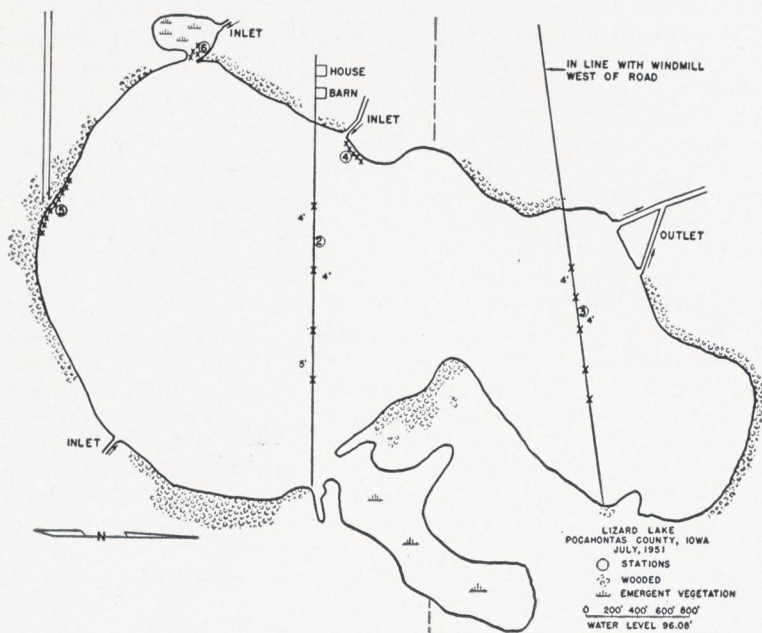


FIG. 1.—Map of Lizard Lake, Pocahontas County, Iowa, showing sampling stations.

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DESCRIPTION OF STATIONS

Six sampling stations were established but station 1 was abandoned early in the study and is not included in the present report. The bottom soils in this paper are designated according to the classification outlined by Roelofs (1944). The higher plants were identified using Fassett (1940) and by comparison with specimens in the Iowa State College herbarium. The algae were identified using Prescott (1951).

Station 2 is a line transect located in the south central part of the lake (fig. 1). The bottom is pulpy peat and the water depth varies from 4 to 5 feet. *Potamogeton pectinatus* was the only plant collected at station 2 and by the middle of August it had formed dense mats on the surface of the entire central portion of the lake.

Station 3 is a line transect located in the north central part of the lake (fig.

1). The bottom is pulpy peat and the average depth of the water is approximately 4 feet. *Potamogeton pectinatus* was also abundant at this station and a filamentous algae, *Rhizoclonium hookeri*, was found entangled among the submerged stems.

Station 4 is located along the wooded south shore (fig. 1). All samples at this station were taken at a water depth of 12 to 18 inches. The bottom is composed of sand and gravel with small amounts of detritus. Station 4 was shaded at all times by the trees along the steep bank and no higher plants were present. A filamentous algae, *Ulothrix* sp. was taken in some of the samples but was not abundant.

Station 5 is located along the west shoreline just north of a ditch flowing into the lake (fig. 1). All samples were taken at a depth of 12 to 18 inches. The bottom is composed of fine sand and clay with small amounts of detritus. Heavy growths of filamentous algae were noted at this station and may possibly be due to nutrients received from the small ditch which flows across an open pasture before reaching the lake. Specimens of algae taken in the bottom samples were: *Cladophora crispata*, *C. fracta*, *Rhizoclonium fontanum* and *Ulothrix* sp. There were sparse growths of *Scirpus validus* and *Eleocharis* sp. at station 5 in July but this vegetation almost entirely disappeared later in the summer.

Station 6 is located in a heavily vegetated, shallow bay at the southwest corner of the lake (fig. 1). All samples were taken at a water depth of 18 to 24 inches. The bottom is composed of fibrous and pulpy peat with small amounts of fine sand. *Potamogeton foliosus* and *Najas flexilis* were the dominant submerged and floating-leaved species at station 6 and formed mats in August and September. The following additional plants were collected: *Scirpus validus*, *S. fluviatilis*, *Utricularia vulgaris*, *Alisma subcordatum*, *Sagittaria latifolia*, *S. sp.*, *Potamogeton pectinatus*, *Polygonum coccineum*, *Sium suave*, *Lemna minor*, *L. trisulca*, and *Spirodela polyrhiza*.

SAMPLING METHODS

Four types of collecting apparatus were used in sampling the bottom fauna of Lizard Lake. A standard Ekman dredge, 6 inches square, was used at the deeper water stations. Petersen, Dendy and stovepipe samplers were used for sampling at depths of 18 to 24 inches along the shore (Welch, 1948). For the stovepipe sampler a 24 inch section of stovepipe having a diameter of 7 inches was used. The complete stovepipe sample was collected by removing the top layers of soil by hand, and mixing the remaining bottom materials with the water in the stovepipe. The mixture of bottom materials and water was removed from the stovepipe with a small hand dipper.

The Dendy, stovepipe and Petersen samples collected at station 4 in September were compared by the method of analysis of variance (table 1). The calculated F value is so low that there is apparently no appreciable difference in the estimates of bottom fauna taken by the three different samplers. Appreciable differences may exist between the methods but because of the excessive variability due to uneven distribution of the organisms these differences remained undetected.

On the assumption that the variance remains constant the minimum

number of samples required to keep the standard error within ten percent of the mean was determined by the formula $N = \frac{100 s^2}{Y^2}$ (table 2).³ Since the

assumption that the variance remains constant is probably not satisfied the formula only gives a rough approximation of the actual number of samples required. Nevertheless the values obtained are useful for comparative purposes.

Time limitations would of course prevent taking such large series of samples but the large values give us an indication of the tremendous variability between samples. Because of the amount of variation, any quantitative generalizations based on a few bottom samples may be subject to a great deal of error. If a standard error with 20 percent of the mean were accepted the number of samples needed would be only one-fourth of those indicated in table 2.

The large value for the Ekman sampler indicates that the bottom in the deeper parts of Lizard Lake is not as homogeneous as was assumed when the stations were set up.

The value of 1,658 samples for the Dendy sampler is out of line even when the large number of samples which can be taken with this sampler is considered. The Dendy samples at station 6 also showed a large range in values (5,793 for 10 samples taken in September). The large range in values brings out a disadvantage of the Dendy sampler which in the author's opinion makes it undesirable for use on a bottom of coarse materials. Because of the uneven nature of the bottom at stations 4 and 6 the distribution of the organisms is not homogeneous but they are scattered in small concentration pockets. The small size of the Dendy makes it possible to hit in and out of these pockets with the result that many of the samples give exaggerated values that are either very high or very low.

All samples were collected during the periods July 11-23, August 13-21,

TABLE 1.—Analysis of variance for sampling methods on the basis of milligrams dry weight per square meter at station 4 in September, 1951, Lizard Lake, Iowa

Source of Variation	Degrees of Freedom	Sum of Square	Mean Square
Between methods	2	268,363	134,182
Within methods	14	14,010,781	1,000,770
F = 0.13408			

TABLE 2.—Number of samples required to keep the standard error within 10 percent of the mean. Based on dry weights of samples taken at stations 2 and 4 in September, 1951.

Sampling Method	N
Dendy	1,658
Stovepipe	54
Petersen	19
Ekman	486

³ Where s = standard deviation and Y = mean.

September 6-10 and October 6, 1951. The bottom materials were washed through 40 mesh screen, placed in jars and preserved in 4 percent formaldehyde. Each sample was labelled and kept separate so that the data could be subjected to statistical analysis. The organisms and plant detritus were separated from the sand in the shore samples by placing the sample in a large tub with water, swirling it vigorously, repeatedly pouring off the suspension of organisms and debris. Slightly greater than 98 percent separation of organisms from the sand was accomplished using this method. The sand was divided into aliquot portions and one-fourth of the total was saved.

For dry weight determination the organisms in each major taxonomic group were divided into size classes and large numbers of each size class were dried to a constant weight in an electric oven at 70°C. The mean of three samples was used to obtain a conversion factor for converting the number of organisms in each sample to the dry weight. The shells of all molluscs were removed with dilute hydrochloric acid before weighing.

QUALITATIVE ANALYSIS OF THE BOTTOM FAUNA

Most of the aquatic invertebrates collected in this study were identified by the author with the use of existing keys. The following authors were followed in the identification of the various specimens collected: Molluca: Eddy and Hodson, 1950; Crustacea: Ward and Whipple, 1918, Pratt, 1935; Ephemeroptera: Needham, Traver and Hsu, 1935; Odonata: Garman, 1927, Needham and Heywood, 1929; Trichoptera: Ross, 1944; Coleoptera: Needham and Needham, 1941; Tendipedidae: Johannsen, 1937a, 1937b, Hauber, 1945a, 1945b, 1947. The Ephemeroptera and Zygoptera were determined from specimens reared to the adult stage. With the exception of the Hemiptera all other aquatic insects were determined from immature specimens. The identifications of the Ephemeroptera were verified by Mr. Eugene W. Hamilton of the University of Nebraska. Mr. Richard C. Froeschner of Iowa State College identified all of the aquatic Hemiptera collected. Particular attention was devoted to the midge family Tendipedidae which appeared to be the most abundant and widespread group of bottom invertebrates in Lizard Lake. The nomenclature followed for the Tendipedidae is that given by Johannsen and Townes (1952).

TURBELLARIA

Several flatworms were collected along the shore on sand and gravel bottom and on sand and clay bottom at a water depth of 12-18 inches.

NEMATODA

Free living nematodes were most abundant in the samples collected on sand and gravel bottom at a water depth of 12-18 inches. A few specimens were collected in shallow water from the sand and clay bottom at station 5 and from the pulpy peat bottom at the deep water stations.

OLIGOCHAETA

Oligochaetes were common at both deep and shallow water stations in Lizard Lake. They were much more abundant at the shallow water stations and the greatest numbers were found in samples taken on a fibrous and pulpy

peat bottom in the heavily vegetated bay at station 6. Although common at the deep water stations during August, September and October, no oligochaetes were found in samples from deep water during July.

HIRUDINEA

No leeches were collected in deep water. They were most abundant in samples collected on sand and gravel, and sand and clay bottom in shallow water. Most of the specimens collected on the sand and gravel bottom at station 5 were attached to small rocks.

The leeches were not included in the quantitative data because extreme variability in size made it impossible to divide them into size groups for weight determination. Because of their relatively large size and low utilization by fish they would tend to confuse the quantitative data from a standpoint of food production. A number of workers have found that fish seldom utilize leeches as food (Bennett, Thompson and Parr, 1940; Leonard, 1940; Howell, 1942; Ball, 1948; Patriarche and Ball, 1949).

MOLLUSCA

Helisoma sp.—Two species of *Helisoma* were collected; one having a shell with rounded whorls and one having whorls with acute shoulders. These snails were most abundant in samples taken in shallow water and they were common in smaller numbers at the deep water stations. Samples taken at station 6 in the heavily vegetated bay contained the largest numbers of *Helisoma* of both species. The species with rounded whorls was most abundant in deep water and the species with acute shoulders was rarely collected in deep water.

Physa sp.—*Physa* was rarely taken in the deep water samples and its distribution was very similar to that of the species of *Helisoma* with acute shoulders.

Anodonta sp.—One specimen collected on the sand and gravel bottom at station 4 in July.

CRUSTACEA

Estheria mexicana Claus.—These shell shrimp were common on the sand and gravel bottom at station 4 and were not found at any other station. Most of the specimens were collected by seining along shore. Only one specimen was collected in the bottom samples.

Hyaella knickerbockeri (Bate).—This little fresh water amphipod was abundant at all the shallow water stations. It was commonly collected where there were growths of filamentous algae and the greatest numbers were found on the heavy growths of filamentous algae at station 5. It was also commonly collected in small numbers at the deep water stations.

Cambarus sp.—One crayfish was collected in a bottom sample at station 4 in July.

HEXAPODA

EPHEMEROPTERA

Mayflies of the family Baetidae were common at all the shallow water stations. Only four specimens were collected in deep water samples. *Caenis forcipata* McDunnough.—Most abundant of the mayflies in the bottom samples from Lizard Lake. Very common at all the shallow water stations during

all sampling periods, with the greatest numbers being collected on the sand and gravel bottom at station 4. *Callibaetis* sp.—Rarely taken in bottom samples. Two specimens collected at station 6 and one at station 5. *Baetis* sp.—Rarely taken in bottom samples. One specimen collected at station 3 and one at station 5.

ZYGOPTERA

Damselflies of the family Coenagrionidae were common in bottom samples collected at both deep and shallow water stations in September and October. Three species were identified from reared specimens: *Enallagma civile* (Hagen), *E. carunculatum* (Morse), and *Ischnura verticalis* (Say). *I. verticalis* and *E. civile* were the most common species taken in bottom samples.

ANISOPTERA

Anax junius (Drury).—Two specimens found in bottom samples taken in the heavily vegetated bay at station 6 in August.

Libellula pulchella (Garman).—Two specimens collected at station 6 in October.

HEMIPTERA

Although the aquatic Hemiptera are not true benthic forms they were quite common in bottom samples from the sand and gravel bottom at station 4 and from the sand and clay bottom at station 5. They were rarely taken at the other stations in Lizard Lake. The following genera and species were identified by Mr. Froeschner: *Corisella tarsalis* (Fieber).—One specimen from station 5 and one from station 4 in July and August respectively. *Trichocorixa kanza* Sailer.—This was the most abundant species of Corixidae collected in bottom samples from Lizard Lake during August and September. *Sigara alternata* (Say).—One specimen collected at station 4 in September. *Palmocorixa buenoi* Abbott.—Several specimens collected at stations 4 and 5. *Notonecta undulata* Say.—Rare in bottom samples. One nymph and one adult collected at station 6 in September. *Buenoa* sp.—Rare in bottom samples. One nymph collected at station 4 in July.

TRICHOPTERA

A few caddis flies were collected in deep water samples but they were most abundant in the shallow water samples.

Leptoceridae: *Oecetis* sp. a of Ross (1944).—Common on sand and gravel bottom at station 4 and on sand and clay bottom at station 5 dwelling in a case constructed of fine particles of sand. *O. inconspicua* (Walker).—Two specimens were collected on sand and gravel bottom at station 4. *O.* sp.—This undetermined species was very abundant in samples taken at stations 4 and 6.

Hydroptilidae: *Agraylea multipunctata* Curtis.—Common at stations 5 and 6. Several specimens were found attached to submerged stems of *Potamogeton pectinatus* in deeper water samples at stations 2 and 3. The fibrous case which was found attached to submerged stems and roots of aquatic plants is pictured by Betten (1934, p. 501).

COLEOPTERA

Aquatic beetle larvae were not common in the bottom samples from Lizard Lake. No adult beetles were taken in the bottom samples. Sixteen specimens representing the following families and genera were collected.

Gyrinidae: *Dineutes* sp.—Nine specimens collected from sand and gravel bottom at station 4 in July and August. Adult *Dineutes assimilis* and *Gyrinus* spp. were common on the surface of the lake in September.

Haliplidae: *Peltodytes* sp.—Four specimens found in samples collected from the heavily vegetated bay at station 6 during July and August. *Haliplus* sp.—One specimen from station 4 and one from station 6 both collected in September.

Dytiscidae: *Laccophilus* sp.—One specimen collected at station 5 in July.

DIPTERA

With the exception of an undetermined puparium which was very abundant at station 4 the only dipterous larvae collected in the bottom samples belonged to the midge family Tendipedidae. Nineteen genera and species representing three subfamilies were identified.

Pelopiinae (= Tanypodinae): *Pentaneura mallochi* (Walley).—Rare in bottom samples. Four specimens collected in September; two from sand and clay bottom and two from sand and gravel bottom. *Pelopia stellata* Coquillett.—One specimen collected in deeper water in August. *Tanypus* sp. b. of Johannsen (1937a).—Common in deeper water at station 3 in July. *Procladius* sp.—Very abundant and most characteristic tendipedid at the deep water stations throughout the sampling period. A few specimens were collected at each of the shallow water stations. All specimens appeared to be of the same species on the basis of larval characters. *Coelotanypus* sp.—Common at deeper water stations during August, September, and October sampling periods. None collected in shallow water.

Hydrobaeninae (= Orthocladiinae): *Hydrobaenus* (*Trichocladus*) *senex* Johannsen.—Rare in bottom samples. Six specimens collected in shallow water at stations 5 and 6. *Cricotopus* sp.—Rare in bottom samples. Several specimens collected in deeper water at station 3 and in shallow water at stations 4 and 6.

Tendipedinae: *Harnischia* (*Harnischia*) *abortiva* (Malloch).—Rare in bottom samples. Collected at both deep water stations and from the fibrous and pulpy peat bottom at station 6. *Tendipes* (*Limnochironomus*) *modestus* (Say).—Rare in bottom samples. One specimen identified from a bottom sample collected at station 6 in July. *T. (Tendipes) tentans* (Fabricius).—Very abundant in samples collected on pulpy peat bottom in deeper water and in samples collected from the fibrous and pulpy peat bottom at station 6. None were collected at stations 4 and 5 in shallow water. This is the largest tendipedid in Lizard Lake and cannot be separated from *T. plumosus* on the basis of larval characters. *T. tentans* should be considered as tentatively occurring in Lizard Lake until rearing experiments have been conducted. *T. plumosus* is considered a profundal form but has been collected in water 3-6 feet in depth (Johannsen, 1937b). *T. (T.) decorus* (Johannsen).—Tentatively identified as *T. decorus* on the basis of size, otherwise inseparable from *T. tentans* and *T. plumosus* on basis of larval characters. Common at stations 6 in August and September. *T. (Limnochironomus)* sp. At least two species of the subgenus *Limnochironomus* occur in Lizard Lake. The very abundant tendipedid fauna at station 4 during July and August was made up almost entirely of a dark green *Limnochironomus*. *T.* sp.—Three unidentified specimens of *Ten-*

dipes having one pair of gills on the eleventh abdominal segment were collected at station 6. *Chironomus (Endochironomus)* spp.—Two specimens of the subgenus *Endochironimus*, as defined by Johannsen (1937b), were collected at station 6 in July and August. *Polypedilum (Polypedilum) illinoense* (Malloch).—Rare in bottom samples. Three specimens collected from deep water stations and four specimens from sand and clay bottom at station 5. *P. sp.*—Several specimens of an undetermined *Polypedilum* were collected at stations 5 and 6. *Glyptotendipes (Glyptotendipes) senilis* (Johannsen).—Rare in bottom samples. Four specimens collected on sand and gravel bottom at station 4 in July. *Cryptochironemus digitatus* (Malloch).—Most abundant and widespread tendipedid collected in the bottom samples at Lizard Lake. Only a few specimens were collected at station 6 but it was abundant at all other stations throughout the sampling period. *Tanytarsus* spp.—Although not abundant this genus was widespread and a few specimens were collected at each of the stations.

HYDRACARINA

Aquatic mites are very difficult to pick from preserved samples and most of them were undoubtedly missed. They occurred in samples from all types of habitat sampled.

QUANTITATIVE ANALYSIS OF THE BOTTOM FAUNA

Because of the large amount of variation between samples taken at the same station the data used in the following analysis probably only give a rough approximation of the true conditions existing in the lake during the sampling period.

DEEP WATER STATIONS

The Tendipedidae or midges, comprising 93.43 percent of the dry weight and 78.57 percent of the numbers were by far the dominant group in the deeper water (table 3). The scud, *Hyalella knickerbockeri*, comprised 13.57 percent of the total number of organisms but contributed only 1.47 percent to the dry weight because of its small size. The other organisms found in the deeper water contributed very little to the total quantity.

Although conditions at stations 2 and 3 appeared to be very similar in regard to bottom soils and vegetation there was a wide difference in the aver-

TABLE 3.—Average dry weight and numbers of organisms per square meter for the deep water stations

	Weight (mg)	Percent	Number	Percent
Tendipedidae	1,280.00	93.44	1,210.00	78.57
Gastropoda	28.30	2.07	39.30	2.55
Oligochaeta	22.30	1.63	34.40	2.23
Hyalella	20.10	1.47	209.00	13.57
Heleidae	6.71	0.50	20.80	1.35
Zygoptera	5.67	0.41	10.90	0.70
Trichoptera	3.64	0.27	7.52	0.49
All others	2.87	0.21	8.35	0.54
Total	1,370		1,540	

age dry weight of organisms at these two stations (table 4). Station 2 supported a greater dry weight of bottom fauna although there was little difference in the average number of organisms at the two stations.

Station 2 and 3 were compared by the method of analysis of variance on the basis of total dry weight for each month in which samples were taken. The results (table 5) indicate that there was a significant difference between the stations in July and August and that the populations were very similar in September and October. The difference in dry weight of organisms at these stations during July and August was caused by the large bloodworm, *Tendipes* (= *Chironomus*) *tentans*, which is the largest tendipedid found in the lake. This species was very abundant at station 2 during July but few were taken in the dredge samples at station 3. In the latter part of July and in early August this species emerged and very few were taken in the dredge samples during September and October at either station.

The maximum numbers and dry weight of bottom fauna per square meter at the deeper water stations were found during the month of July with the minimum during September (fig. 2). The October dredgings showed a large increase in numbers but a very small increase in dry weight. Since the fauna of the deep water stations is composed largely of the larvae of Tendipedidae the variation in total fauna follows the variation in this group. The steep fluctuations in the quantity of bottom fauna from month to month can be

TABLE 4.—Average number and dry weight of bottom fauna per square meter at stations 2 and 3 during July, August, September and October, 1951

Station	Number	Weight (mg)
2	1,575	1,873
3	1,517	870

TABLE 5.—Analysis of variance for stations 2 and 3 on the basis of milligrams dry weight per square meter

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square
Ignoring months			
Between stations	1	32,075,992	32,075,992*
Within stations	57	86,268,534	1,513,483
July			
Between stations	1	17,532,160	17,532,160*
Within stations	11	8,053,684	732,153
August			
Between stations	1	2,545,465	2,545,465*
Within stations	15	7,872,820	524,855
September			
Between stations	1	20,085	20,085
Within stations	18	752,413	41,801
October			
Between stations	1	14,553	14,553
Within stations	7	910,714	130,102

* Significant at 5 percent level.

explained by the annual life cycle of tendipedid egg, larvae, pupae and emergence.

The minimum at the deep water stations in Lizard Lake was reached in September after the emergence of *Tendipes tentans*. Other species grew into the fauna during October causing a slight increase. That these specimens were small early instar larvae is indicated by the very slight increase in weight as compared with the increase in numbers (fig. 2). Although it cannot be definitely established with the present data it appears that the October increase is due to the growth into the fauna of early spring and early summer emerging species. The maxima in both numbers and weight would probably be reached in early spring before the emergence of these species and after the growth of *Tendipes tentans* back into the fauna.

SHALLOW WATER STATIONS

The shore area of Lizard Lake is a region of extreme variation in habitat and as a result almost all of the major groups of aquatic organisms normally found in a lake are represented (table 7). No single group completely dominated this region as was found to be true in the deeper water. The first four groups, Tendipedidae, Gastropoda, Oligochaeta and *Hyalella* are the same but there is a great deal of difference in their relative proportions as compared with the deep water stations. The Gastropoda are the dominant group contrib-

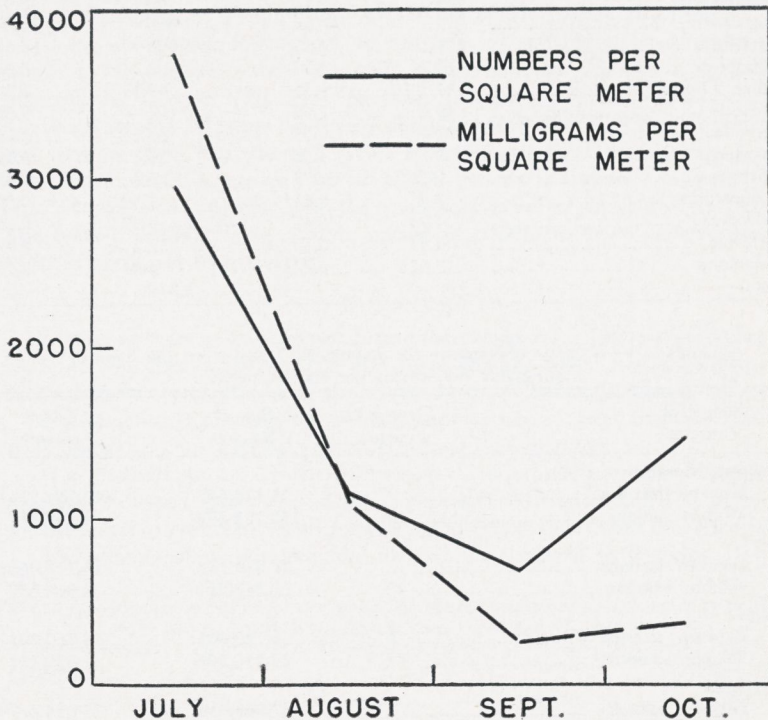


Fig. 2.—Monthly variation in bottom fauna at deep water stations 2 and 3 in Lizard Lake.

uting 36.23 percent to the total dry weight. The Tendipedidae are very numerous but are represented by small species. The "Other Diptera" listed in Table 6 are unidentified puparia which were abundant at some of the stations but were not present in deep water

Comparison of the stations.—The three shore stations, selected for study as represented of the major types of habitat in Lizard, were compared by the method of analysis of variance on the basis of dry weight in milligrams per square meter. (table 7). The calculated F values are significant at the 5 percent level for each month in which samples were taken. This means that we can reject a hypothesis that the populations at all three stations are the same, with the probability that less than 5 percent of the time we would be wrong in rejecting such a hypothesis. As was true for the deep water stations the differences between stations were due mainly to the size of the organisms rather than any great differences in numbers (table 8).

The uneven gravel bottom at station 4 yielded the largest number of organ-

TABLE 6.—Average dry weight and numbers of organisms per square meter for the Stations 4, 5, and 6.

	Weight (mg)	Percent	Number	Percent
Gastropoda	255	36.23	391	10.24
Tendipedidae	483	19.12	1,160	30.41
Oligochaeta	235	17.62	436	11.44
Hyalella	131	9.82	1,400	36.69
Anisoptera	63.2	4.74	8.73	0.23
Other Diptera	47.1	3.53	49.5	1.30
Baetidae	39.6	2.97	191	5.00
Corixidae	34.6	2.59	87.6	2.29
Zygoptera	15.7	1.18	21.1	0.55
Trichoptera	9.78	0.73	17.9	0.47
Notonectidae	8.11	0.61	3.52	0.09
Coleoptera	4.93	0.37	5.47	0.14
Heleidae	4.31	0.32	37.2	0.97
Nematoda	2.32	0.17	6.81	0.18
Total	1,334		3,819	

TABLE 7.—Analysis of variance for stations 4, 5 and 6 on the basis of milligrams dry weight per square meter.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square
Ignoring Months			
Between stations	2	23,128,647	11,564,324*
Within stations	82	149,228,876	1,819,864
July			
Between stations	2	27,434,132	13,717,066*
Within stations	12	23,862,861	1,988,572
August			
Between stations	2	8,720,005	4,360,002*
Within stations	22	12,110,808	550,491
September			
Between stations	2	22,068,439	11,034,219*
Within stations	42	57,133,480	1,360,321

* Significant at the 5 percent level.

isms and all the major groups found in the lake were represented at this station. Rawson (1930) found that in Lake Simcoe the highest populations of bottom organisms were in the protected stony bays. In Lizard Lake this type of habitat is most closely approximated by conditions at station 4 where the gravel bottom provides a large surface area of habitat for the bottom organisms. Small larvae of Tendipedidae, Oligochaeta and the naiads of the mayfly family Baetidae were the dominant organisms at station 4.

The quantity of bottom fauna from the heavily vegetated peat bottom at station 6 was much higher on a basis of total dry weight because of the large bloodworm, *Tendipes tentans*, which was very abundant on this type of bottom. Another factor contributing to the high average weight were the Odonata which were most abundant at station 6 and contributed disproportionately to the total weight in relation to their numbers.

The sand and clay bottom at station 5 was the poorest producer of bottom fauna on the basis of dry weight. The abundance of *Hyaella* sp. and Corixidae on the filamentous algae at this station resulted in the high numerical count (3,856 per square meter).

After the maximum in July there were no major fluctuations in the weight of the shallow water fauna (fig. 3), due to the small size of the majority of the species represented and to the overlapping in the periods of abundance of many different species. The high value in July was mainly a result of the very marked abundance of Tendipedidae (7,350 per square meter) at station 4.

There were sharp fluctuations in numbers of organisms from month to month in the shallow water zone with a maximum in July and a minimum value during October (fig. 3). The sharp increase in September was caused by several factors. Mayflies were very abundant at station 4 during September and most of them had emerged before samples were taken in October. Large mats of filamentous algae had settled to the bottom at station 5 in September and this algae was swarming with the small crustacean, *Hyaella knickerbockeri*. The bottom samples taken at this station in September gave an estimate of 5,410 *Hyaella* per square meter.

SUMMARY

Bottom samples were collected during the period from July 9 to October 6, 1951, at two deep water stations and three shallow water stations which are believed to be representative of the major types of habitat in Lizard Lake.

The magnitude of variation between samples was so great that any quantitative generalizations may be subject to a great deal of error.

A statistical comparison of the Petersen, Dendy and stovepipe methods of sampling indicated that there was no appreciable difference in the quantity of bottom fauna as estimated by these three samplers on a sand and gravel bottom.

The number of samples required to keep the standard error within 10 per-

TABLE 8.—Average number and dry weight of bottom fauna per square meter at Stations 4, 5 and 6 during July, August, September and October, 1951

Station	Number	Weight (mg)
4	4,108	1,297
5	3,856	671
6	3,497	1,846

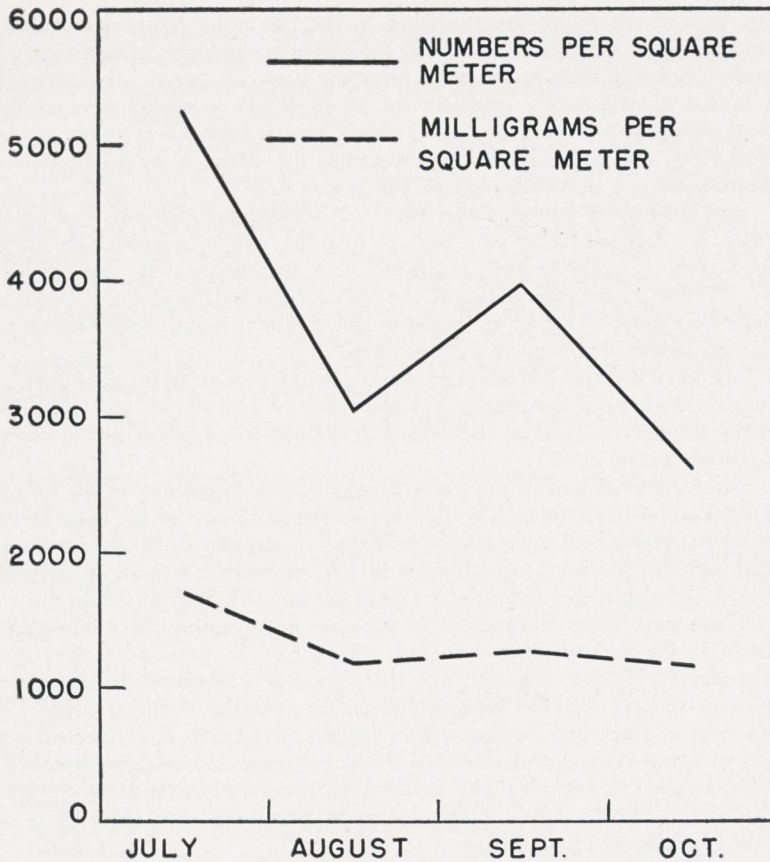


Fig. 3.—Monthly variation in bottom fauna at shallow water stations 4, 5 and 6, Lizard Lake.

cent of the mean was found to be 1,658 for the Dendy, 486 for the Ekman, 54 for the stovepipe and 19 for the Petersen.

On the basis of average dry weight of organisms the greatest quantities of bottom fauna were produced on the pulpy peat bottom in the deeper part of the lake (1,873 mg per square meter) and on the fibrous peat bottom in a heavily vegetated bay (1,846 mg per square meter).

A bottom composed of sand and clay produced the lowest average quantity of bottom fauna (671 mg per square meter).

A sand and gravel bottom in shallow water produced the largest numbers (4,108 per square meter) and kinds of organisms but was intermediate on the basis of average dry weight (1,297 mg per square meter), because of the small average size of the organisms represented.

The peak of abundance occurred in July with the minima in September or October.

The Tendipedidae were the most abundant group of aquatic invertebrates

and comprised 93.44 percent of the total dry weight at the deep water stations.

Gastropoda (36.23 percent), Tendipedidae (19.12 percent) and Oligochaeta (17.62 percent) were the most important components of the bottom fauna at the shallow water stations.

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SOME OBSERVATIONS ON THE EFFECTS OF WATER
INFLOW AND OUTFLOW ON THE PLANKTON OF SMALL
LAKES

BY A. J. BROOK AND W. B. WOODWARD

Brown Trout Research Laboratory, Pitlochry, Scotland

(With 7 Figures in the Text)

INTRODUCTION

Of the factors which determine the abundance of the plankton in a lake it is believed that the flow of water through the lake may at times be of over-riding importance. In fact many small lakes may be regarded as parts of river or stream systems in which the flow of water has been temporarily impeded. Studies of the plankton of flowing waters indicate that the quantity of their plankton is inversely proportional to the current speed (Brook & Rzóska 1954, Rzóska, Brook & Prowse 1955). The magnitude of the influence of the flow of water through a lake will depend on the volume of the lake, the extent of its catchment area and the amount of rainfall on this area. Thus the effect will be greatest in a small shallow lake with a large catchment area receiving high rainfall, and will become less significant the bigger the lake and the smaller the catchment area and rainfall. For purposes of comparison, a figure representing the replacement of water in a lake may be determined by dividing the volume of water contained in the lake by the amount of water passing through for a given period. This *replacement quotient* has been expressed in the following paper in days. Clearly, in any lake an increase in the standing crop of plankton will indicate that the rate of increase of the plankton is greater than the diluting effect of the replacement water, though the converse may not be true, for this may be due to the death of plankton. Hence the productivity of a lake with a rapid replacement of water may actually be greater than that of a lake with a slow replacement though standing crop estimates may suggest the contrary.

The effect of the flow through may, however, be modified by a number of factors. For example, although the annual rainfall on the catchment area is of prime importance, its incidence may also be significant. A short period of heavy rain will have a greater effect than the same amount of rain spread over a longer period. The topography, geology and vegetation of the catchment area will affect the speed of run-off and the proportion of the rainfall that actually runs into the lake. A number of small inlets bringing in the same amount of water as one large inlet may produce a very different result. The effect in lakes with inflowing streams opposite those flowing out will differ considerably from those with inflows near the outflow. Other morphological features of the lake, such as the size and distribution of islands and weed-beds may either confine or spread the inflowing water.

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R. J. B.

THE EFFECTS OF DROUGHT CONDITIONS ON
THE FISH AND BOTTOM ORGANISMS OF
TWO SMALL OXBOW PONDS

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THE EFFECTS OF DROUGHT CONDITIONS ON THE FISH AND BOTTOM ORGANISMS OF TWO SMALL OXBOW PONDS

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DESCRIPTION OF AREA

Two oxbow ponds of Squaw Creek, located in Boone County, Iowa, were formed in 1952 when the stream was straightened in building a new bridge. The two oxbows are separated from the creek by an earthen fill and from each other by a road grade. Although there is no direct connection between the two ponds, they become united through overflow waters of Squaw Creek during flood periods.

The ponds are bordered by steep banks and wooded areas on the east and by wooded pastures on the west. Cattle use two areas of the south pond for watering. The north pond does not have watering areas easily accessible to the cattle.

The south pond normally has a surface area of approximately one acre and an average depth of three feet. The north pond normally has a surface area of two acres and an average depth of four feet. The water supply of these oxbows is maintained by run-off, seepage, and flooding from the creek.

The bottom deposits of both ponds are mainly of silt with sand and gravel in isolated areas. Many tree stumps and dead trunks are present in the north pond and the bottoms are covered with dead leaves.

The bulk of the fish population in the oxbows consisted of: carp, *Cyprinus carpio*; black bullheads, *Ameiurus m. melas*; bluntnose minnows, *Pimephales notatus*; and fathead minnows, *Pimephales p. promelas*. In addition, the following species were found: common white sucker, *Catostomus c. commersoni*; western golden shiner, *Notemigonus chrysoleucas auratus*; northern creek chub, *Semotilus a. atromaculatus*; central bigmouth shiner, *Notropis d. dorsalis*; stone cat, *Noturus flavus*; green sunfish, *Lepomis cyanellus*; orange-spotted sunfish, *Lepomis humilis*; white crappie, *Pomoxis annularis*; and central johnny darter, *Etheostoma n. nigrum*.

The water level in the creek was high enough to enter these ponds on July 14, 1955, and by July 19 the water levels had receded and the ponds were no longer connected with the creek. The south pond was rotenoned on July 19, eliminating all fish that had moved in from the creek during the flood. The bottom fauna in this pond was thus freed of predation by fish during the ensuing drought. Rains during July and August did not add enough water to the pond to raise the water level and by September the area was undergoing a severe drought.

EFFECT OF DROUGHT ON THE
BOTTOM FAUNA

Bottom organisms in the south pond were fairly abundant in November, 1954, but dropped off considerably during the summer probably due to the emergence of insects (Table 1). Rotenone treatment apparently did not affect the bottom fauna. The population on July 21, after treatment, was almost identical to that found July 18, before treatment. Furthermore, the samples of July 21 were picked without preservation and no dead bottom fauna organisms were found. By September 13 the area of the pond was much reduced and some of the sampling stations were no longer under water. By the first week in October the south pond was completely dry. The high population of bottom fauna per quarter-square foot in September is probably partly the normal fall increase in bottom fauna and partly the result of concentration of the organisms into a smaller area, without predation by fish.

Nematodes constituted a small part of the bottom fauna of the south pond. These worms were not taken in numbers large enough to draw conclusions concerning concentrations of the bottom fauna due to the drought.

Oligochaetes comprised 34.1% of the samples by number and 11.5% by volume. Concentration of oligochaetes during the drought was not observed. The average number per bottom sample was about the same before and during the drought.

Several clam shrimps (Order Conchostraca) were collected in the south pond during the second appli-

cation of rotenone on May 28, 1955. Only one specimen was collected in the routine bottom sampling (June 3, 1955).

Two species of mayfly nymphs, *Hexagenia limbata* and *Leptophlebia* sp., were collected from the south pond during November, 1954. A large emergence of *Hexagenia limbata* occurred during May 24-26, 1955. On May 28, 1955, the pond was treated with rotenone. No mayfly nymphs were taken in bottom samples following treatment of the pond with rotenone. No dead mayfly nymphs were found, but the surface of the pond was literally covered with exuviae. In September, 1955, only three mayfly nymphs, *Leptophlebia* sp., were collected in the bottom samples.

Dragonfly nymphs were not taken in bottom samples from the south pond during the normal water levels, but the 7 bottom samples taken on September 13, 1955, during the drought contained 15 dragonfly nymphs (Family Libellulidae).

Concentration of bottom organisms due to the drought was best exhibited by chironomid larvae, ceratopogonid larvae, and *Chaoborus punctipennis*. Dipterous larvae constituted 50.3% by number of the samples collected during normal water levels and 92.4% by number of the samples collected during the drought. In September the south pond contained large numbers of *Notonecta undulata* (Family Notonectidae) and *Arctocorisa* sp. (Family Corixidae), making it impossible to collect a bottom sample that did not contain 20 to 30 notonectids and corixids. These forms were not counted or measured in the bottom fauna as recorded in Table 1.

TABLE 1.—Numbers and Volume of Bottom Fauna Organisms Collected in One-Fourth-Square-Foot Samples from the South Oxbow Pond, Boone County, Iowa.

Date	No. samples	No. organisms per sample			Volume in cubic centimeters		
		Mean	Standard deviation	Range	Mean	Standard deviation	Range
Nov. 9, 1954.....	10	98	65	24-232	0.64	0.76	0.01-2.30
Nov. 27, 1954.....	10	64	29	28-114	0.39	0.28	0.02-0.85
June 3, 1955.....	10	19	10	5-42	0.05	0.09	Trace-0.30
July 18, 1955.....	10	28	17	11-63	0.04	0.025	0.01-0.07
July 21, 1955.....	10	27	22	6-69	0.04	0.023	0.01-0.07
Sept. 13, 1955.....	7	208	85	116-365	0.97	0.69	0.26-2.11

Additional bottom samples were taken from areas of the south pond no longer under water on September 13, 1955. Samples of mud were collected to a depth of 12 inches. The mud samples were collected in layers approximately three inches thick and washed through a sieve to determine if the bottom fauna organisms had penetrated deeper into the mud. No macroscopic organisms were found in these samples. Within two weeks this pond was completely dry.

On November 9, 1955, a series of ten bottom samples were taken from the north pond. Each sample contained at least five leeches identified as *Epobdella* sp. On November 10 another series of ten bottom samples was taken. This group contained a total of five leeches. On November 11 no leeches were present in another series of bottom samples. Sampling to a depth of six inches in the mud failed to locate leeches.

EFFECTS OF DROUGHT ON THE FISHES

The upper end of the north pond was dry by the latter part of Sep-

tember. Many fishes were trapped in drying isolated pools and soon died; fishes over 6.0 inches in total length were not found. The larger fish may have been taken earlier by predators which apparently abounded in the area as evidenced by the number of tracks of herons and raccoons.

By October 27, 1955, this 2-acre pond had been reduced to one large pool 150 by 20 feet with an average depth of 9 to 12 inches. The color of the water was black and the bottom mud had an oily odor. Large numbers of bullheads, fathead minnows, bluntnose minnows, and orange-spotted sunfish were gulping air at the surface of the pool. The dissolved oxygen content of the water at this time was 0.2 p.p.m. The dissolved oxygen content of this pool was again determined on October 31 and on November 8, and each time was found to be 0.2 p.p.m.

On November 8, 1955, the bottom of the north pond contained dead white suckers, creek chubs, bluntnose minnows, fathead minnows, bullheads, orange-spotted sunfish, and green sunfish. Two prostrated carp (15.0 inches, total length) were

retrieved from the surface of the pond. A thin ice cover which had formed on November 8, 1955, probably served to protect the dying fish from predators.

By November 8, 1955, some water was again present in the south pond and the water level of the north pond was no longer dropping. As the temperature dropped and evaporation ceased to be an important source of water loss, the water from small springs began entering the pond.

The concentration of fishes in the remaining water area on November 12 was so great that Ekman dredge samples collected from this pool all contained live bullheads. Some dead fishes were also taken in the bottom samples.

WINTER EFFECTS ON THE DROUGHT-SHRUNKEN POND

By November 17 a three-inch ice cover had formed on the pond. Areas of thin ice near the bank and around logs contained large concentrations of minnows and bullheads. Continuation of the severe cold weather resulted in the formation of a six to nine inch ice-cover by November 28. Many of the fishes utilizing the small open areas around the logs were found with the lower halves of their bodies frozen in the ice and the upper halves exposed. The exposed halves of the bodies had been eaten away by predators, leaving the heads and backbones intact.

By December 28 the pond had completely frozen to the bottom and the bottom mud had frozen to a depth exceeding nine inches. Fishes were found frozen into the ice and the ice had a strong "fishy" smell due to decomposition of the fishes.

The dark color of the bullheads absorbed heat and some decomposition was occurring even when the surrounding ice was solid.

Thirteen holes, approximately 18 by 18 inches, were cut and the fishes frozen into the ice were counted. The ice was arbitrarily marked off into three zones: upper two inches of ice, intermediate zone, and frozen bottom mud with the lower two inches of ice. No fishes were found frozen in the upper two inches of ice. In the intermediate zone 105 bullheads, 7 central bigmouth shiners, and 4 fathead minnows were found. In the lower zone 6 bigmouth shiners, 4 bluntnose minnows, and 25 fathead minnows were found.

Two possible explanations may be advanced to explain the presence of bullheads in the upper portions of the ice and the minnows in the lower portions of the ice and bottom muds. The minnows may have succumbed to the adverse conditions in the pond first and the ability of the bullheads to gulp air may have kept them near the ice until they were trapped there and frozen. A second explanation may be that the bullheads prevented the minnows from utilizing the area immediately under the ice.

Chironomid larvae were present in the frozen mud, and a sample of this mud was returned to the laboratory. Water was placed in the pail containing the frozen mud and it was allowed to thaw out to room temperature. All macroscopic bottom organisms in this sample of mud were dead.

Above-freezing temperatures during the last of February melted ice and snow, and by March 1, 1956, both oxbows were again completely

covered with 12 inches of water. Fifteen seine hauls made in the north pond contained no live fish, but a total of 55 dead fish were collected in the seine hauls—45 bullheads, 9 fathead minnows and 1 orange-spotted sunfish.

Eighteen bottom samples were taken in the north pond and ten bottom samples were taken in the south pond. No live macroscopic bottom forms were found.

DISCUSSION

The destruction of the fish population and the macroscopic bottom fauna population of the two oxbow ponds apparently was complete.

Restocking of the two oxbows with fish is dependent on Squaw Creek overflowing into the ponds during the high-water periods and on fish survival in Squaw Creek. Preliminary spring field data collected from Squaw Creek indicate a low survival rate of fishes, but the extent of survival has not been determined.

The repopulation of the two oxbows by the bottom organisms will not be dependent on the overflow of Squaw Creek into the ponds, but will be dependent on the amount of survival of the bottom fauna in the creek. Most of the bottom fauna organisms have adult forms capable of repopulating the isolated pools.

SUMMARY

Severe drought conditions in Boone County, Iowa, resulted in the complete drying of a 1-acre oxbow and in reducing a 2-acre oxbow to one large pool 150 by 20 feet.

As the water levels receded in the south pond a concentration of the

bottom fauna, mainly dipterous larvae, was observed. By the latter part of September this pond was dry and the macroscopic bottom fauna was apparently destroyed.

As the water levels receded in the north pond many fishes were stranded in isolated pools and died when the isolated pools dried up. The remainder of the fish population was concentrated in the last remaining pool. Severe winter conditions resulted in the complete freezing of the pool resulting in the destruction of the fish population.

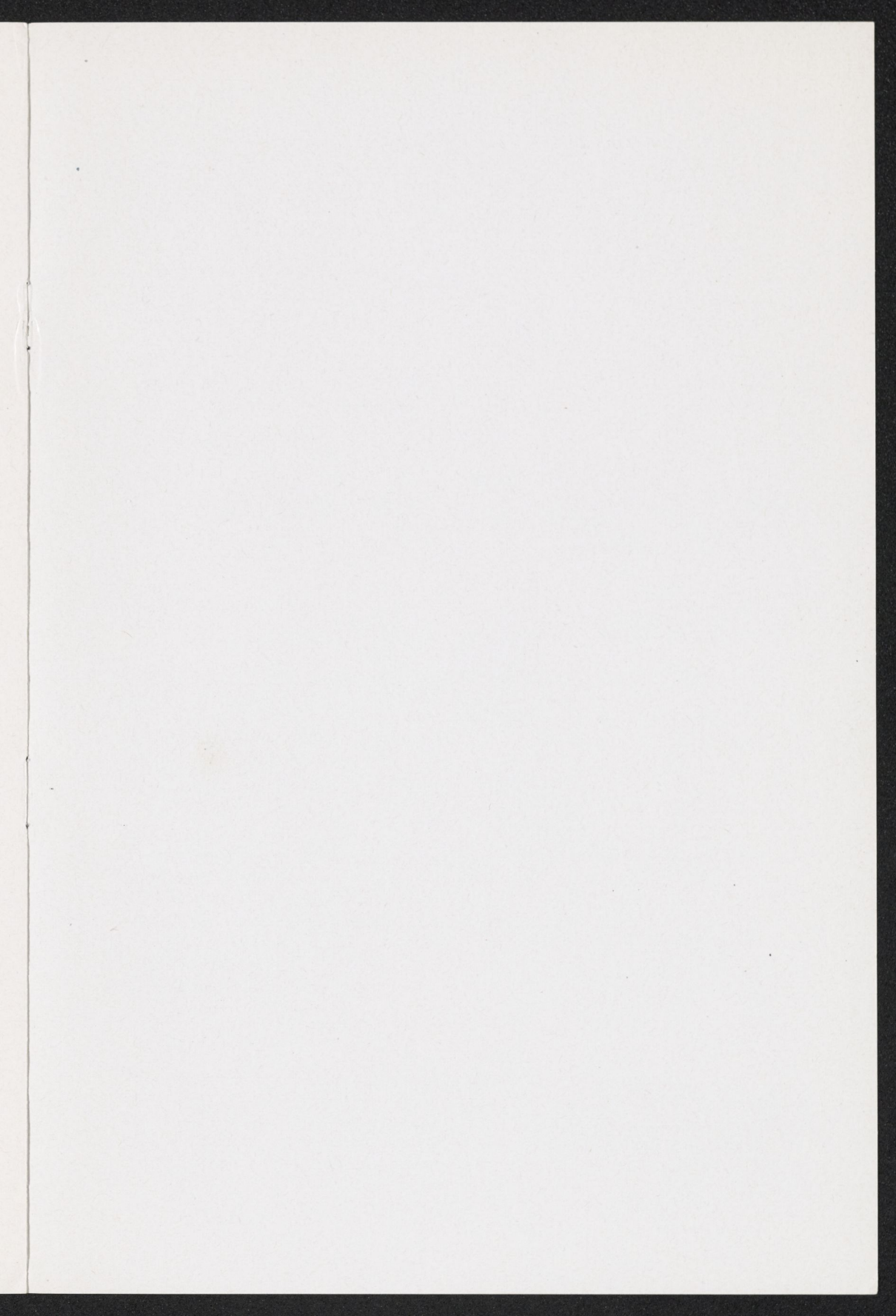
Bullheads were concentrated in the intermediate zone of the ice and the minnows were located in the lower two inches of ice and in the frozen bottom muds. Apparently all fishes and macroscopic bottom fauna organisms were killed.

Repopulation of the two oxbows by fishes and bottom fauna organisms will be dependent on the amount of survival of fishes and bottom organisms in Squaw Creek.

ACKNOWLEDGMENTS

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Notes on the Precision of Numerical and Volumetric Plankton Estimates from Small-sample Concentrates¹

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ABSTRACT

Standard enumeration and volumetric determination techniques were employed to measure littoral plankton in a shallow prairie lake. Numerical and volumetric estimates were obtained from two-liter water samples which had their plankton (and tripton) content concentrated by means of a continuous-flow centrifuge.

Microplankton were enumerated, and their volumes were calculated on a species and total basis employing a two-stage sampling scheme. Distributions of various species in Sedgwick-Rafter cell mounts from four representative samples (containing at least 73 species) were examined. Occurrences of certain forms in the "fields" of Sedgwick-Rafter cell mounts conformed very closely to the Poisson series while others departed significantly. A majority of the latter were adequately fitted by the negative binomial distribution. For illustrative purposes, totals of selected species distributed as Poisson and negative binomial were estimated and assigned confidence limits. The value of the contagion or over-dispersion factor, $1/k$, in constructing confidence limits was pointed out. In addition, the sample size required to yield an estimate having a specified precision was computed for a selected species distributed as Poisson. It was generally concluded that the error of estimated individual species totals usually greatly exceeds the desired level. Hence the size of subsample necessary to secure reasonably precise estimates for the numbers of *each* microplankton species in a given sample concentrate would be, as a rule, quite unwieldy.

Total microplankton counts per subsample were assumed to be normally distributed. Applications of standard statistical techniques indicated that efficiency in the two-stage sampling scheme is most effectively increased by including counts from additional primary sampling units (Sedgwick-Rafter cell mounts). The most practical subsampling ratio from the standpoint of increasing the precision of over-all numerical estimates without expending additional time and labor appeared to be four cell mounts and ten micrometer "fields" per mount.

Microplankton volumetric determinations were made employing a "calculated" volume method. The precision of volumetric unit counts for individual species was indeterminate because of the unknown distribution of the volumetric units. A lack of knowledge concerning such contagious distributions precludes a rigorous assessment of the "calculated" volume's utility.

Macroplankton were counted and had their volume calculated in a manner similar to that described for the microplankton except that the elementary sampling unit constituted an entire Sedgwick-Rafter cell mount. Very adequate numerical and volumetric estimates of individual macroplankton species and total macroplankton were secured from counts and measurements in only three cell mounts per sample concentrate. It was determined that had the allowable error of estimate been relaxed to 20 per cent (\pm) of the true value, on the average, a sample size of only one cell mount would have sufficed for estimating total macroplankton.

INTRODUCTION

The quantitative assessment of marine and fresh-water plankton populations presents many difficulties, which have received considerable attention since the inception

of plankton research. Any biological population with as complex a structure as that of a mixed plankton population is difficult to evaluate. Several studies (*e.g.*, Littleford *et al.* 1940, Gilbert 1942, Serfling 1947, and

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Ballentine 1953) have shown that mechanical errors or those errors arising from manipulation of sample material can, in many cases, be removed or at least reduced by improving collection and preparation techniques. Sampling errors and random variation due to the distribution of the plankters in prepared mounts can often be accounted for by measuring the precision of sample estimates and, if necessary, using this information to modify counting techniques through changes in sampling design.

The present paper represents an attempt to evaluate the plankton techniques employed in a recent study concerned with numerical and volumetric measurement of littoral plankton populations (Kutkuhn 1956). Due to its great volume, it was not practical to subject the sample data to complete statistical treatment. However, to give some insight as to the over-all reliability of the estimates, data from four series of plankton samples chosen as being representative of the type examined during the study were subjected to extensive statistical analysis. The results of this analysis presented herein not only serve to place the findings of the parent study on a firmer basis, but may also have some value as a guide for future plankton studies.

The author extends sincere gratitude to Dr. K. D. Carlander, Iowa State College, for his many helpful suggestions and numerous courtesies. Special thanks are due Drs. J. D. Dodd, Iowa State College, and W. T. Edmondson, University of Washington, for verifying identifications of certain plankton organisms, and Prof. P. G. Homeyer, Iowa State College Statistical Laboratory, for critically reading an early draft of the manuscript.

COLLECTION, CONCENTRATION, AND PREPARATION OF SAMPLE MATERIAL

Water samples for plankton analyses (Table 1) were secured by submerging a two and one-half liter wide-mouth bottle until filled to the two-liter mark. Because of time limitations only a single sample was taken during each sampling period. Thus it was necessary to assume that, for all

TABLE 1. Collection data for the four plankton samples selected for statistical analysis

Each consisted of a two-liter water sample taken from the littoral zone of North Twin Lake, Iowa, August 1955

Sample number	I	II	III	IV
Date collected	8-2-55	8-2-55	8-2-55	8-4-55
Time collected	8 a.m.	2 p.m.	8 p.m.	2 a.m.
Water temperature	84°F	85°F	84°F	83°F
Air temperature	81°F	85°F	83°F	74°F
Water depth	2 ft.	1 ft.	3 ft.	2½ ft.
Sample depth	½ ft.	½ ft.	½ ft.	½ ft.
Location	East shore	East shore	West shore	West shore
Wind	S:0-3 mph	SSW:0-3 mph	SSE:0-5 mph	Calm

practical purposes, a single sample contained a reasonable representation of the plankton populations actually occurring at the sampling station during the sampling period.

Immediately following its removal from the lake and prior to fixation, the plankton in each water sample was concentrated to about 15 milliliters using a Foerst continuous-flow centrifuge (1955 model: about 20,000 rpm). The centrifuging rate was standardized at about one liter per eight minutes. Very satisfactory fixation was obtained for practically all plankters by flooding the concentrate with 5 ml of very hot 20% formalin solution.

When compared with the plankton net and sedimentation methods, centrifuging was found to be the most rapid and efficient means for concentrating even the smallest nanoplankton. Possible errors in estimates arising from the loss of unusually buoyant forms were assumed negligible since frequent re-centrifugations revealed the loss of such forms during initial centrifuging to be minimal. These extra-buoyant forms were mainly certain blue-green algae (*e.g.*, *Microcystis aeruginosa*) which occurred in relatively small amounts in most samples. Losses of sample material through adhesion to apparatus were minimized by consistently using clean glassware. Undue aggregation caused by compaction during the centrifuging process was never a serious problem. Such a condition could usually be remedied by adding a small quantity of weak detergent solution and properly diluting the concentrate.

Primärproduktion und Seetypen

WILHELM RODHE (Uppsala, Schweden)

Mit 10 Abbildungen und 4 Tabellen im Text und auf 3 Beilagen

Schon in den Anfängen der Erforschung der biologischen Seetypen wurde das Ausmaß der organischen Produktion als ein Hauptmerkmal betrachtet und besonders die Produktion des Phytoplanktons ins Auge gefaßt: Geringproduktion der Planktonalgen in oligotrophen Seen, Hochproduktion in eutrophen (NAUMANN 1917). Da aber die Größe dieser Produktion, welche prinzipiell die Zeit mit einschließt, früher nur schwierig und unsicher ermittelt werden konnte, setzte man gewöhnlich — bewußt oder unbewußt — an ihre Stelle die jeweils vorhandene Quantität (Biomasse) des Phytoplanktons. Die Vermischung des dynamischen Aspektes mit dem statischen und die Verwischung ihrer grundsätzlichen Unterschiede ist jedoch aus sowohl begrifflichen wie anderen Gesichtspunkten zu vermeiden. Erst in neuerer Zeit wurde auf Grund von theoretischen Erwägungen mehr beachtet, daß nicht die momentan vorhandene Biomasse des Phytoplanktons, sondern die davon je Zeiteinheit neugebildete organische Substanz den für die Beurteilung des dynamischen Stoffwechselsystems wichtigeren Begriff darstellt (vgl. u. a. LINDEMAN 1942, ÅBERG und RODHE 1942, CLARKE 1946, ELSTER 1954).

Die vor wenigen Jahren von E. STEEMANN NIELSEN (1952, 1954) eingeführte C¹⁴-Methode zur direkten Bestimmung der primären Produktion organischer Substanz (organischen Kohlenstoffs) im freien Wasser gibt uns nunmehr die ersehnte Möglichkeit, in einer einfachen, zugleich sehr empfindlichen und genauen Weise die photosynthetische Leistung des Phytoplanktons festzustellen. Seit 1953 wird die C¹⁴-Methode, kombiniert mit gleichzeitigen Zählungen zur Bestimmung der Zusammensetzung und der Biomasse des Phytoplanktons, im Limnologischen Institut in Uppsala und dessen Laboratorium am Erken intensiv benutzt, um die Primärproduktion und ihre Bedingungen besonders im Erken, aber auch in einigen anderen Seen Schwedens — soweit möglich — aufzuklären. Die ausführlichen Berichte über die Ergebnisse dieser Untersuchungen sind noch in Vorbereitung, aber einige für die in dieser Session behandelten Seetypenfragen interessante Resultate können schon hier in Kürze gebracht werden.

Einige Schwierigkeiten bei der Auswertung der C¹⁴-Daten

Zunächst seien als Beispiele einige Diagramme der Vertikalverteilung der Primärproduktion gegeben (Fig. 1 und 2). Die ihnen zugrundeliegenden Werte

(Punkte) sind erhalten durch 24stündige Versuche im See selbst, wo 125ml-Flaschen, beschickt mit Wasser aus verschiedenen Tiefen nebst je 1 ml unorganischer C^{14} -Lösung, von kurz nach Sonnenuntergang eines Tages bis zum Sonnenuntergang des folgenden Tages in Tiefen entsprechend den Probenentnahmen ausgehängt wurden. Durch graphische Integrierung ist aus den Kurven die Primärproduktion in jeder Meterschicht ($mg\ C_{ass}/m^3$) zu bestimmen, und die Summierung dieser Werte für die ganze trophogene Säule ergibt die Primärproduktion je Flächeneinheit des Sees ($mg\ C_{ass}/m^2$) während des Versuchstages.

Hier soll nicht näher auf die Fehlerquellen in der Auswertung der an sich zuverlässigen C^{14} -Methode eingegangen werden, sondern einige kurze Bemerkungen mögen dabei genügen. Es wird noch diskutiert (vgl. STEEMANN NIELSEN 1956, RYTHER 1956), ob die erhaltenen Werte die Brutto- oder die Nettoproduktion angeben; bis diese Frage geklärt ist, müssen die Absolutwerte mit Vorsicht interpretiert werden. Zu berücksichtigen ist auch, daß die Assimilation in geschlossenen und in gewisse Tiefen versenkten Flaschen nicht unbedingt identisch ist mit der gleichzeitigen Assimilation in den entsprechenden Schichten der umgebenden Wassersäule, wo die Planktonalgen durch Strömungen und Turbulenz stetig mehr oder weniger in Bewegung gehalten werden und deshalb wechselnde Tiefen einnehmen. Da die hemmende Wirkung hoher Lichtintensitäten mit verlängerter Expositionszeit zunimmt, erhält man mit ganztägigen Assimilationsversuchen in der Regel zu niedrige Werte für die oberen Schichten. Besonders wenn die Wassermasse stark bewegt ist und die individuellen Algen sich nur ganz kurze Zeit in der Oberflächenschicht aufhalten können, entsprechen stark ausgeprägte Optimumkurven (vgl. Erken, 11. 5. 1955) in ihrem Hemmungsteil kaum den tatsächlichen Verhältnissen im freien Wasser.

Optimumkurven, wie man sie vom Frühjahr bis spät in den Herbst an klaren oder nicht zu stark wolkigen Tagen erhält, sind aber für die vorliegende Fragestellung besonders wertvoll. In der Schicht optimalen Lichtgenusses müssen nämlich vorwiegend die stofflichen Voraussetzungen, die „Fruchtbarkeit des Wassers“, ausschlaggebend sein für die Größe der Produktion des jeweiligen Phytoplanktonbestandes. Ein Vergleich verschiedener Seen auf Basis ihrer Primärproduktion in der Schicht des Lichtoptimums ($mg\ C_{ass}/m^3$, max., vgl. Fig. 1 und 2) sollte demnach für die Charakterisierung der Seen ebenso wichtige Hinweise geben können wie der Vergleich ihrer Primärproduktion je Oberflächeneinheit. Aus dem vorhandenen Material von mehr als 100 vollständigen C^{14} -Serien *in situ* habe ich deshalb zum näheren Studium 75 Optimumkurven von 9 Seen herausgegriffen (Erken 36, Görvåln 13, Ransaren 10, Kultsjön 9, Nedre Laksjön 2, Övre Laksjön 2, Katterjaure, Vassijaure und Torne träsk je 1 Kurve). Erken und Görvåln liegen in Uppland, östlich bzw. südlich von Uppsala, Ransaren und Kultsjön im südlichen Lappland und die übrigen fünf Seen im nördlichen Lappland unweit Abisko.

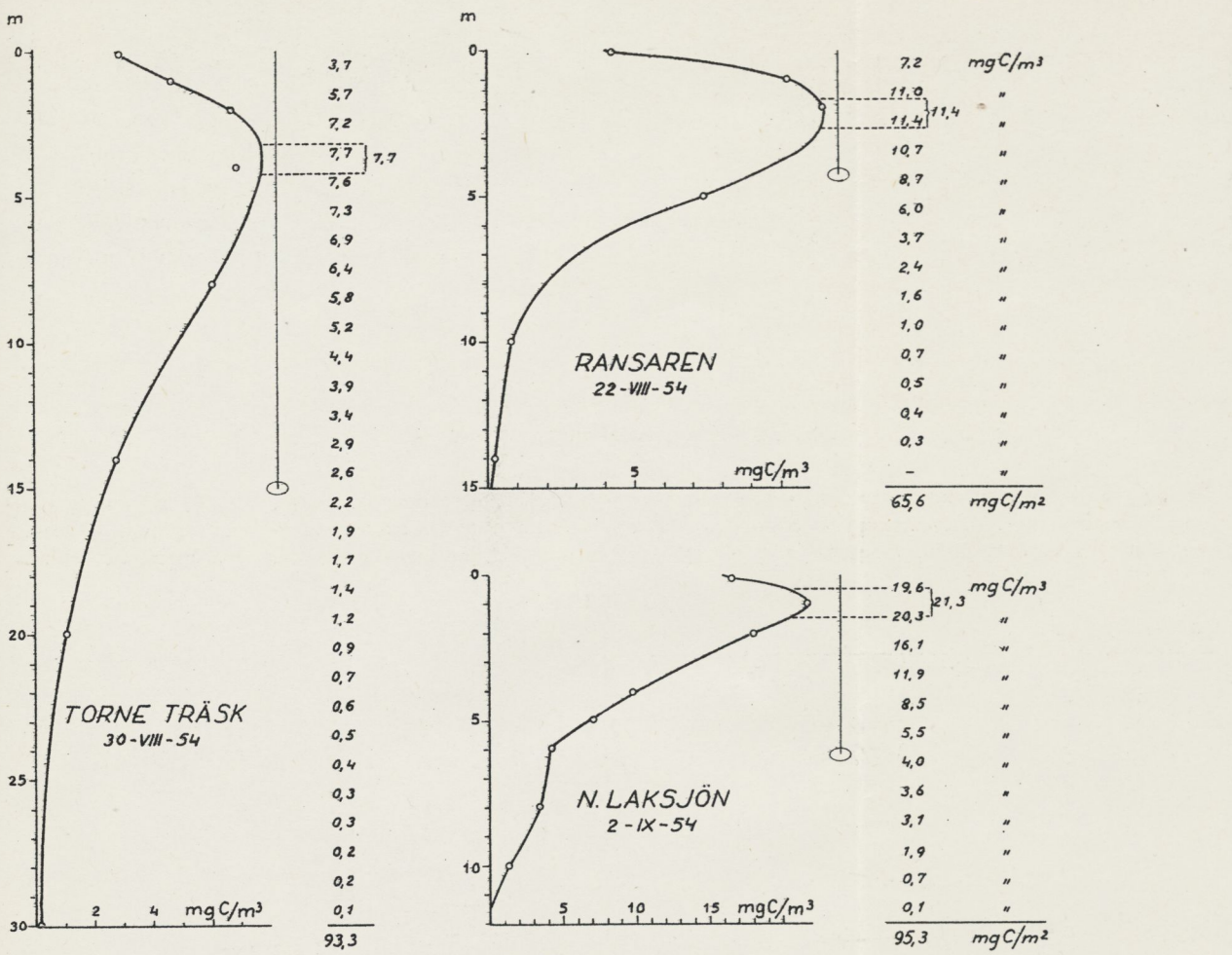


Fig. 1

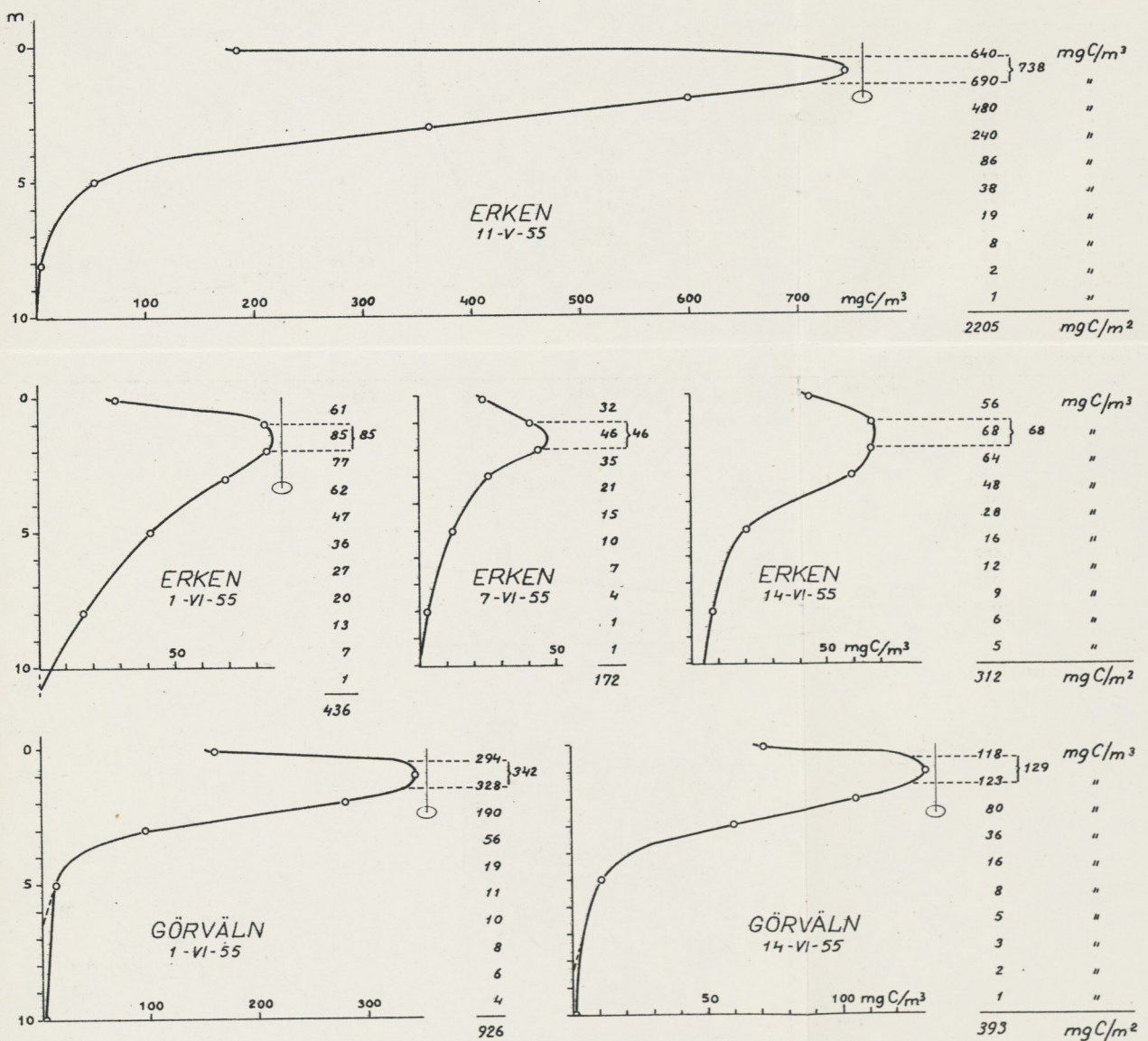
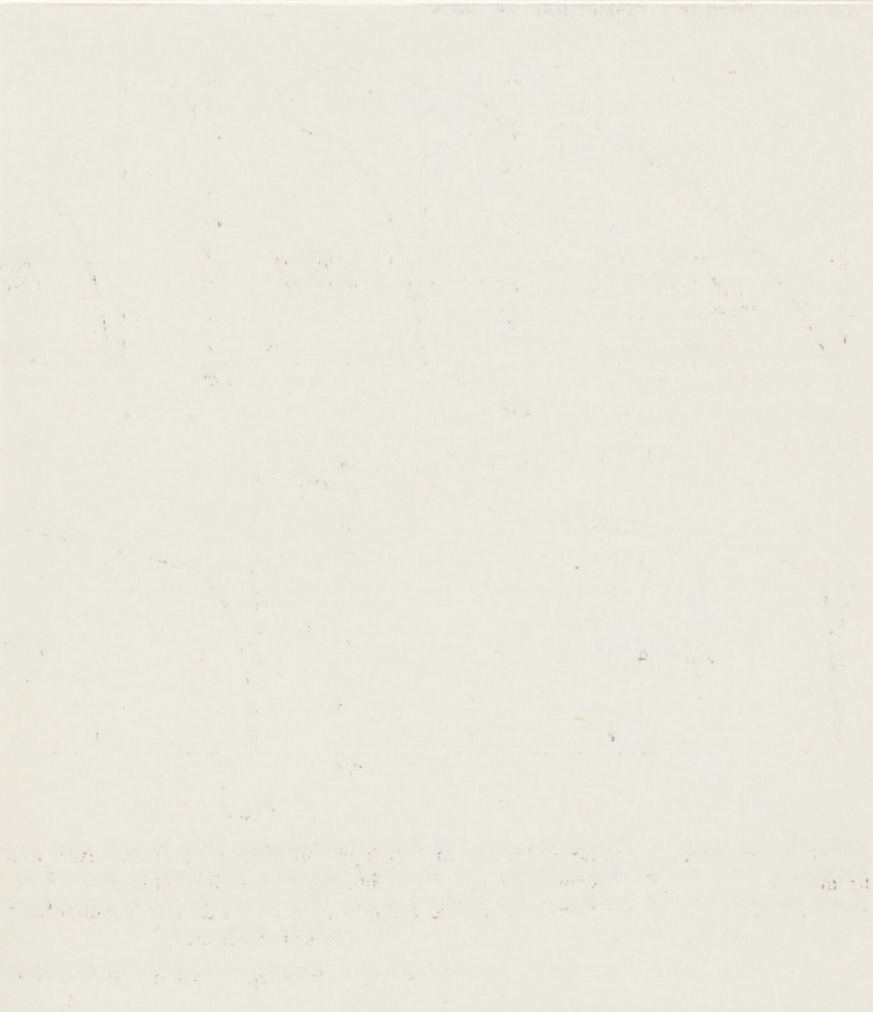
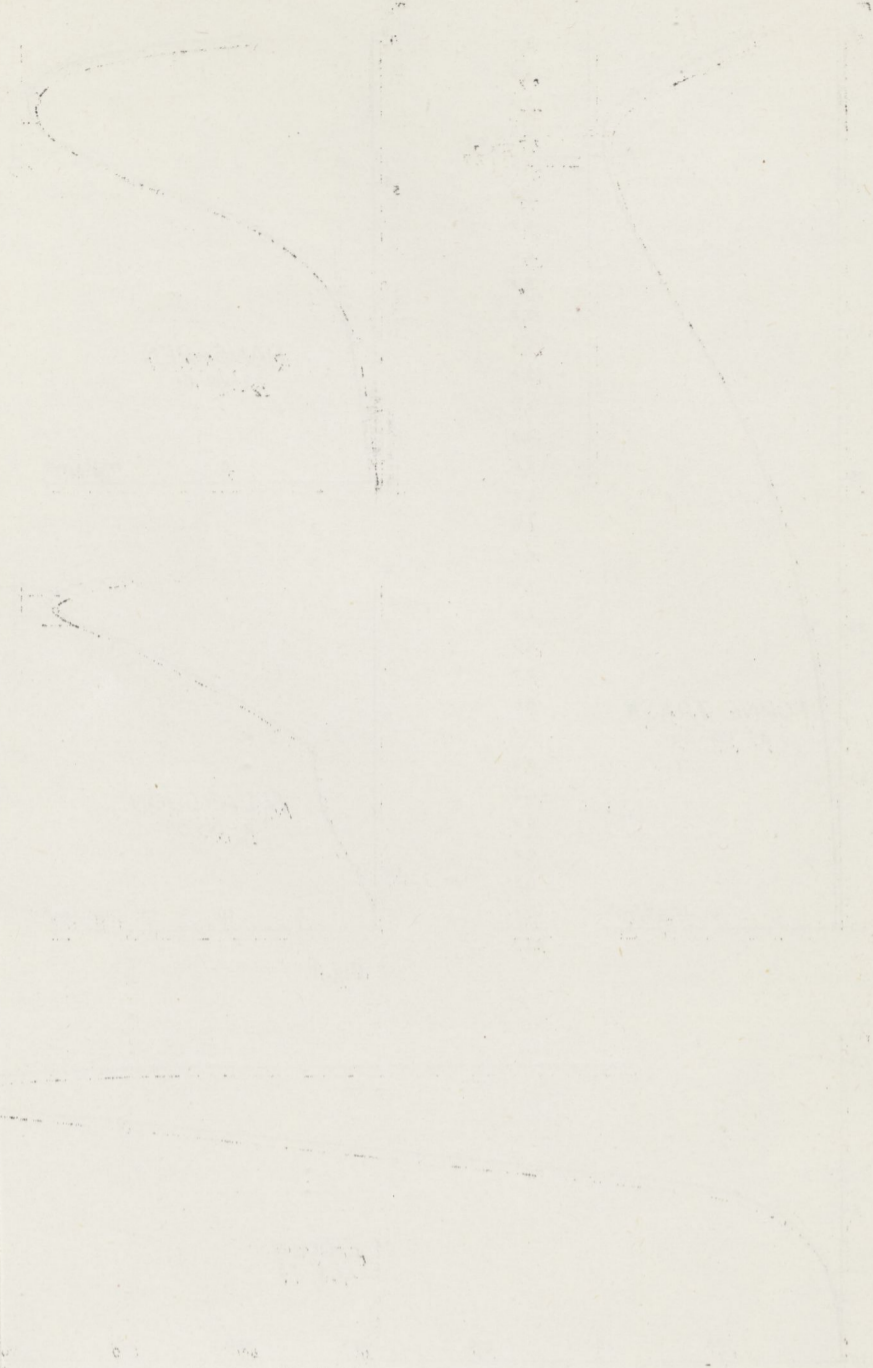


Fig. 2

Beispiele der täglichen Primärproduktion in drei lappländischen (Fig. 1) und zwei uppländischen (Fig. 2) Seen. Neben den Klammern wird der Produktionswert für den lichtoptimalen Kubikmeter angegeben (berechnet nach der Kurve). — Der Knick im unteren Teil der Kurve für Nedre Laksjön (Fig. 1) wurde durch Anhäufung des Phytoplanktons in der Sprungschicht verursacht.



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Tabelle 1.

	A	B	C	D	E = C · D	F	G = A/B	H = A/D	I = B/E
	Produktion (je Tag)		Tropho- gene Schicht	Frischgewicht		Sichttiefe	V/O- Quotient	Aktivitäts- koeffizienten für Frischgewicht	
	mg C/m ³ (max.)	mg C/m ²	m	mg/m ³ Mittel	mg/m ²	m		je m ³ (max.)	je m ²
Torne träsk 16. 8. 1954	7,7	93,3	30	102	3 060	15,0	0,08	0,08	0,03
Ransaren 22. 8. 1955	11,4	65,6	15	138	2 070	8,7	0,17	0,08	0,03
Nedre Laksjön 2. 9. 1954	21,3	95,3	11	1 900	20 900	6,2	0,22	0,01	0,005
Erken 11. 5. 1955	738	2205	10	11 000	110 000	2,0	0,34	0,07	0,02
Erken 1. 6. 1955	85	436	11	1 390	15 300	4,1	0,20	0,06	0,03
Erken 7. 6. 1955	46	172	10	465	4 650	—	0,27	0,10	0,04
Erken 14. 6. 1955	68	312	10	790	7 900	—	0,22	0,09	0,04
Görvåln 1. 6. 1955	342	926	6*	3 800	22 800	2,4	0,37	0,09	0,04
Görvåln 14. 6. 1955	129	393	7*	1 160	8 100	2,6	0,33	0,11	0,05

* Dunkelassimilation in den tiefsten C¹⁴-Flaschen (vgl. Fig. 2).

Schon ein Blick auf die in Fig. 1 und 2 und in Tab. 1 gegebenen Beispiele zeigt, daß die Primärproduktion der verschiedenen Seen sehr verschieden ist oder sein kann. Die Unterschiede sind aber nicht nur regionaler Art, denn im selben See treten oft große, mehr oder weniger kurzfristige Veränderungen auf. Solche können selbstverständlich durch die temporale Abwandlung des Phytoplanktons und der Produktionsbedingungen veranlaßt werden (wie bei den vier wiedergegebenen Serien für Erken 1955: vom Maximum der Frühjahrsproduktion Mitte Mai über ein Minimum Anfang Juni bis zum neuen Anstieg eine Woche später), und die konsekutiven C^{14} -Serien geben dann den wirklichen Produktionsverlauf der Sukzession wieder. Andererseits kommen aber auch, besonders im Hoch- und Spätsommer, wenn die größeren und koloniebildenden Planktonalgen ihre Hauptentwicklung haben, sogar von Tag zu Tag sehr große Variationen vor, die ihren eigentlichen Grund in einer unregelmäßigen Horizontalverteilung („patchiness“) des Phytoplanktons haben und durch windbedingte Wassermassenverschiebungen zustande kommen (RODHE, VOLLENWEIDER und NAUWERCK 1958). Konsekutive Werte schildern in diesem Falle nicht einen temporalen Vorgang in einer einheitlichen Wassermasse, und es ist dann kaum möglich, durch fortlaufende Serien an einer einzigen Stelle ein wirklich repräsentatives Bild des zeitlichen Geschehens im See als Ganzheit zu erhalten.

Obgleich somit mehrere Umstände Schwierigkeiten in den Weg legen, wenn man Produktionsdaten aus verschiedenen Seen in regionaler und absoluter Hinsicht auswerten will, soll nun doch ein Versuch in dieser Richtung gemacht werden.

Vergleich der maximalen Produktion je Volumen mit der gleichzeitigen Produktion je Fläche

Aus den Diagrammen in Fig. 1 und 2 ist ersichtlich, daß die Form und die vertikale Ausdehnung der Produktionskurven mit der Sichttiefe, d. h. mit den optischen Eigenschaften des Wassers, in Verbindung stehen. Um die beiden Extreme der dargestellten Kurven hervorzunehmen, so reichte in Torne träsk, wo die Sichttiefe 15 m war, die trophogene Schicht bis etwa 30 m, und die Zone annähernd optimalen Lichtes war dann mehrere Meter dick, mit ihrem Schwerpunkt bei 4 m. In Erken am 11. Mai 1955 dagegen, bei einer Sichttiefe von 2 m, war die untere Grenze der Primärproduktion bei etwa 10 m; das auf eine dünne Schicht zusammengedrückte Maximum lag bei 1 m Tiefe. (Die exakte Festlegung der unteren Grenze der trophogenen Schicht stößt — zum Teil auch wegen Dunkelassimilation, vgl. Fig. 2: Görvåln — auf Schwierigkeiten, die hier nicht erörtert werden können.) Als ein Index der Kurvenform kann offenbar der Anteil des höchstproduktiven Kubikmeters an der Gesamtproduktion der trophogenen Wassersäule, d. h. das Verhältnis zwischen $mg\ C/m^3$, max., und $mg\ C/m^2$, benutzt werden. Dieser „V/O-Quotient“ beträgt für Torne träsk $7,7/93,3 = 0,083$, für die genannte Erkenkurve $738/2205 = 0,335$, was mit anderen Worten bedeutet,

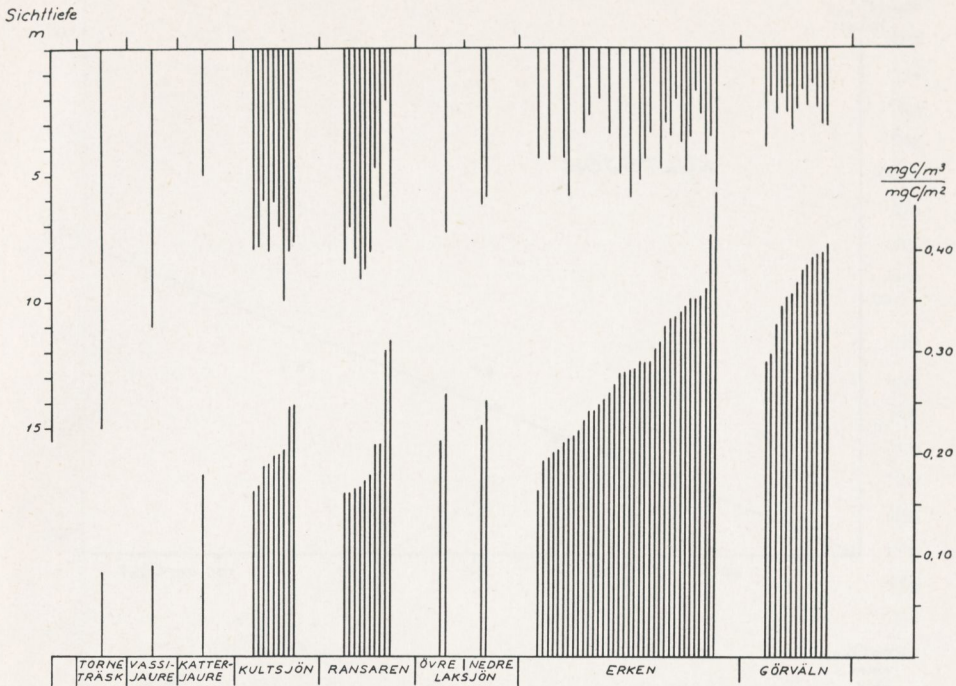


Fig. 3. Unten. Anteil des lichtoptimalen Kubikmeters an der täglichen Primärproduktion der trophogenen Schicht; die Werte sind für jeden See in steigender Reihenfolge geordnet. — Oben. Zugehörige Sichttiefenwerte.

daß in der Zone des Lichtoptimums die Produktion je Kubikmeter 8,3⁰/₀ bzw. 33,5⁰/₀ der totalen Produktion ausmachte. Für die anderen Kurven von Fig. 1 und 2 sind die entsprechenden Werte aus Tab. 1 zu entnehmen, und die V/O-Quotienten sämtlicher hier benutzten C¹⁴-Serien sind zusammen mit den zugehörigen Sichttiefen (soweit vorhanden) in Fig. 3 veranschaulicht.

Die näheren Beziehungen zwischen Sichttiefe und Primärproduktion sollen hier nicht behandelt werden, da Dr. VOLLENWEIDER in seinem gleich folgenden Vortrag (VOLLENWEIDER 1958) diesbezügliche Fragen besprechen wird. Wir begnügen uns, an Hand von Fig. 3 festzustellen, daß mit abnehmender Sichttiefe durchschnittlich immer mehr der Gesamtproduktion auf den höchstproduktiven Kubikmeter der Säule fällt, daß also die Optimumkurve der Primärproduktion durchschnittlich um so mehr heterograd wird, je geringer die Sichttiefe. Da diese nur ein rohes Maß der Strahlungsdurchlässigkeit ist und da die Lichtabhängigkeit des Phytoplanktons u. a. artbedingt ist, kann man nicht eine strikte Korrelation zwischen Sichttiefe und V/O-Quotient der Primärproduktion erwarten. Es ist somit verständlich, daß wir in Fig. 3 zahlreiche Fälle finden, die von der generellen Tendenz abweichen.

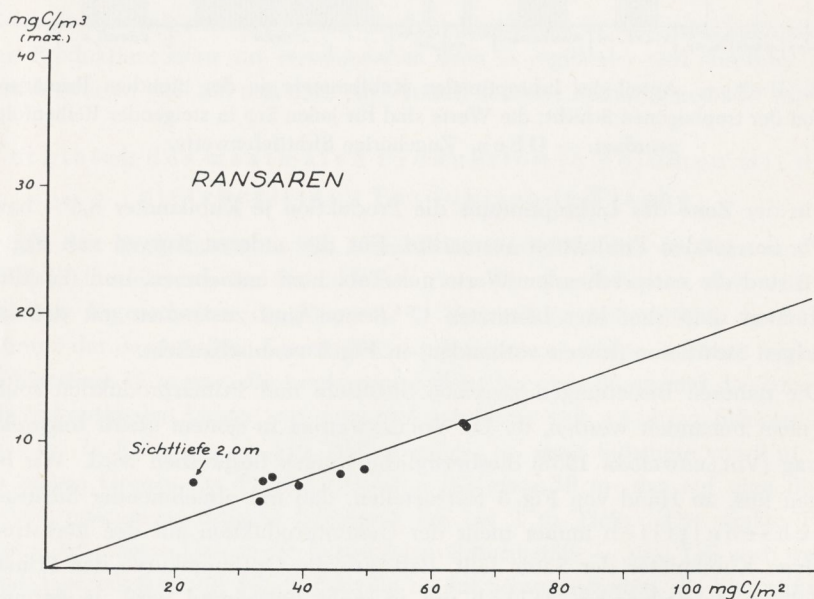
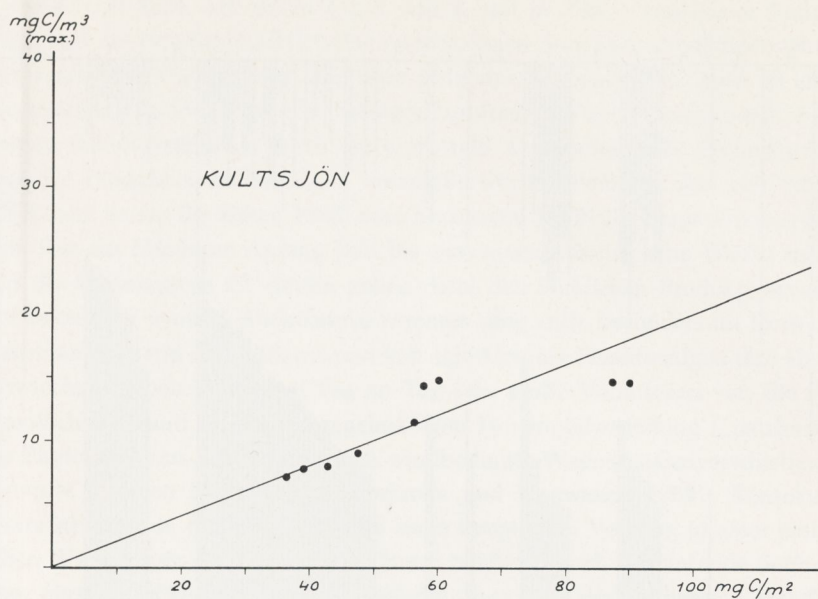


Fig. 4—7. Die Beziehung zwischen der täglichen Primärproduktion des lichtoptimalen Kubikmeters und der gleichzeitigen Primärproduktion in der ganzen Wassersäule: in zwei geringproduktiven Seen mit einer Sichttiefe von meistens 6 bis 8 m (Fig. 4 und 5) und in zwei Seen mit höherer Produktion und Sichttiefe zwischen 2 und 5 m (Fig. 6 und 7). Bemerke den Unterschied im Maßstab zwischen Fig. 4—5 einerseits und Fig. 6—7 andererseits.

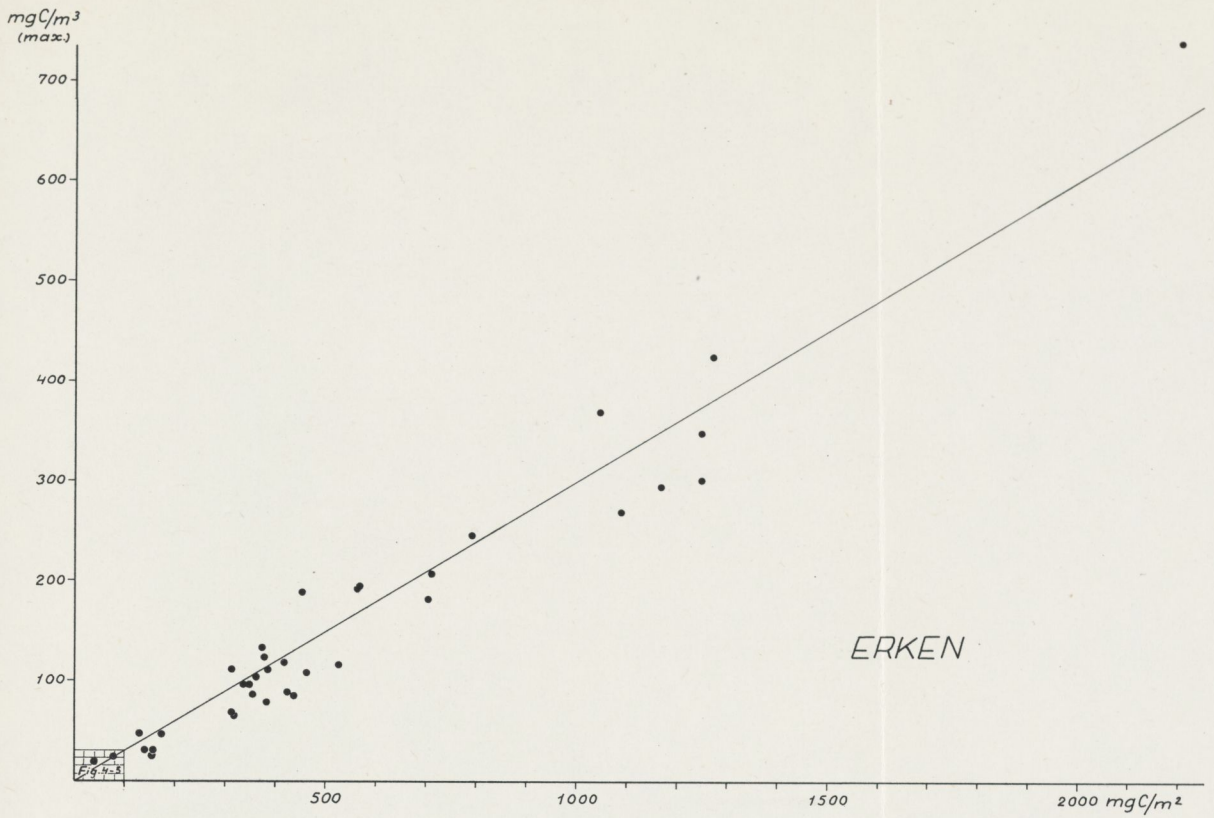


Fig. 6

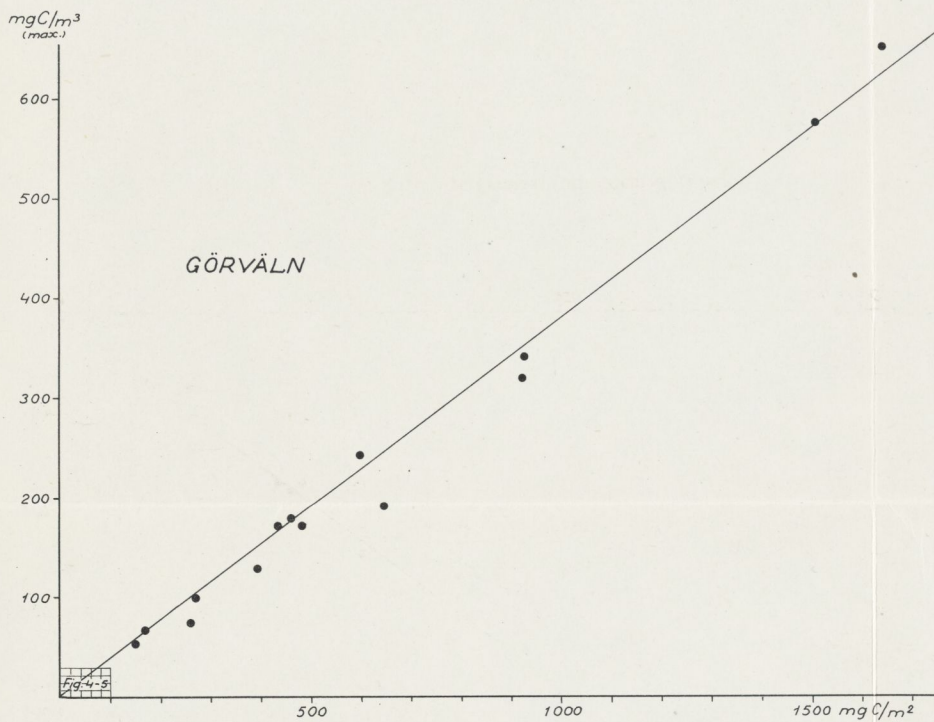
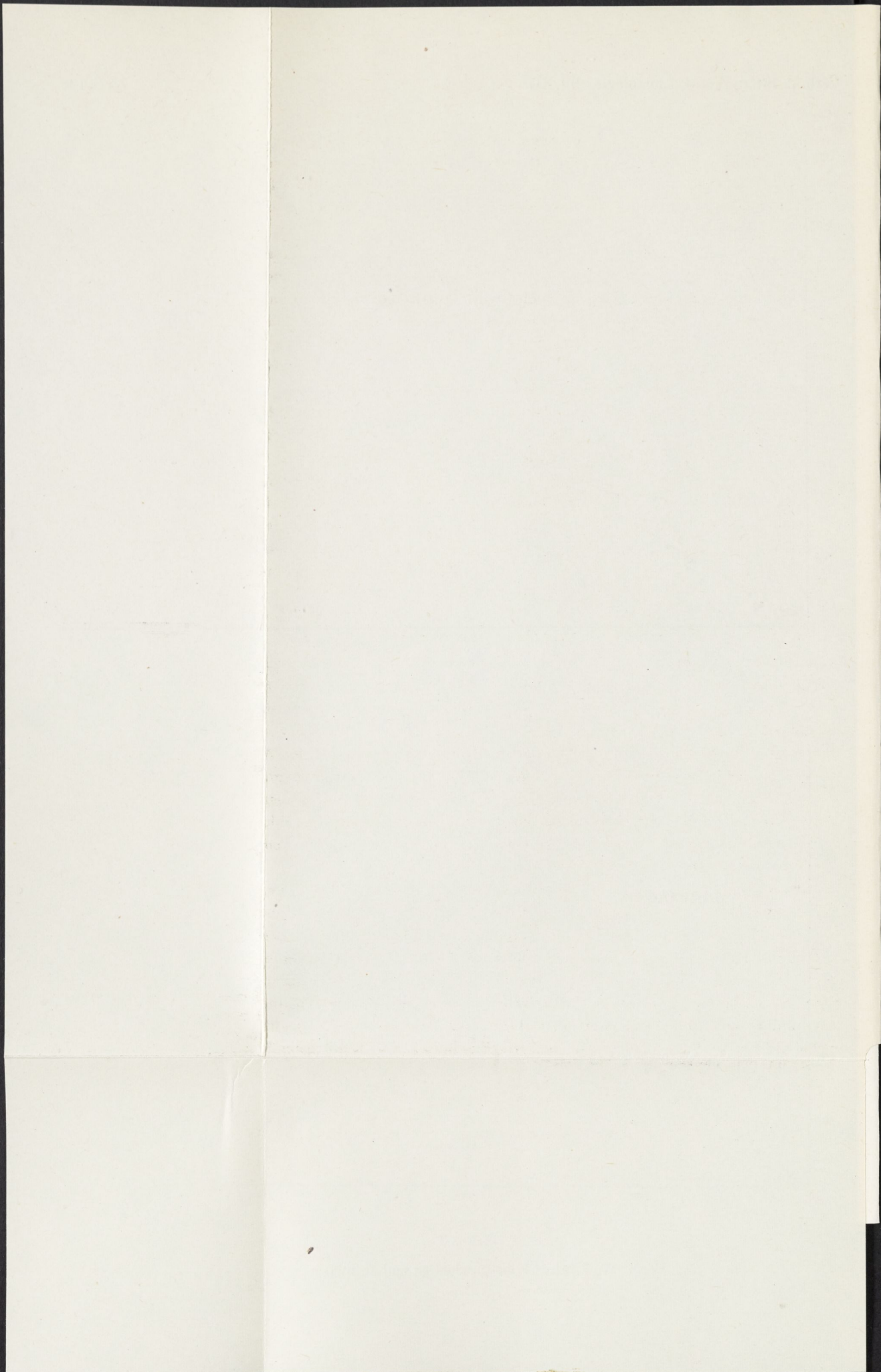


Fig. 7



Die Streuung der V/O-Quotienten tritt mehr in den Hintergrund, wenn wir für den einzelnen See die Absolutwerte der maximalen Produktion je Kubikmeter und der Gesamtproduktion je Quadratmeter einander gegenüberstellen (Fig. 4 bis 7). In den Diagrammen für Ransaren, Kultsjön und Görvälän liegen die meisten Punkte so regelmäßig, daß eine repräsentative Gerade mit hoher Sicherheit für jeden See gezogen werden kann. Auch statistisch ergibt sich, daß in Ransaren durchschnittlich 18%, in Kultsjön 20% und in Görvälän 38% der Gesamtproduktion im höchstproduktiven Kubikmeter ausgeführt wird. Für Erken, wo die Streuung der Einzelwerte größer ist, entspricht die statistisch berechnete Linie einem durchschnittlichen V/O-Quotienten von 30%.

Mit Hilfe von logarithmischen Koordinaten können wir das ganze Intervall der Produktionswerte, von den lappländischen zu den uppländischen Seen, auf einem Diagramm unterbringen (Fig. 8). Mit Rücksicht auf die erheblichen Größenunterschiede (von 23 bis etwa 2200 mg C/m² und von 4,5 bis etwa 750 mg C/m³) ist der Gesamteindruck des Materials recht einheitlich; nur im untersten Bereich, wo die logarithmische Darstellung auch kleine Abweichungen hervortreten läßt, liegen einige Werte etwas außerhalb der Punktwolke. Hätte das Material mehr Werte aus geringproduktiven Seen mit sehr hoher Sichttiefe einerseits und allochthoner Trübung oder Humusfarbe andererseits umfaßt, dann würde die Punktverteilung im niedrigsten Teil gewiß fächerförmige Ausbreitungen nach unten bzw. oben zeigen.

Primärproduktion und Biomasse des Phytoplanktons

Zugleich mit den Produktionsversuchen mit C¹⁴ wurde in den meisten Fällen auch die quantitative Zusammensetzung des jeweiligen Phytoplanktons bestimmt. Durch Multiplikation der Frequenzzahl jeder Art mit dem Volumen der gezählten Einheit (Zelle oder Kolonie) und Summierung der Volumina sämtlicher Arten ist dann das Gesamtvolumen festgestellt worden. Unter der approximativen Annahme, daß das spezifische Gewicht der Algen = 1 ist, wird statt Gesamtvolumen das Frischgewicht als Maß der Biomasse des Phytoplanktons gebraucht, ausgedrückt teils als mg/m³ (= Mittelwert der aus der trophogenen Schicht gezählten Proben), teils als mg/m²; der letztere Wert wurde dabei bis zur unteren Grenze der trophogenen Schicht berechnet (vgl. Tab. 1).

Es wurde zuerst von FINDENEGG (1943) und dann von RUTTNER (1952) gezeigt, daß die Gesamtmenge des Phytoplanktons in oligotrophen Seen je Flächeneinheit gerechnet ebenso hoch sein kann wie in eutrophen Seen, obgleich ihre Biomasse je Volumeneinheit geringer ist. In dem vorliegenden Material, in dem jedoch nur der Bestand in der trophogenen Schicht berücksichtigt wird, ist es auch auffällig (vgl. Tab. 1), daß die Unterschiede z. B. zwischen Torne träsk und Ransaren einerseits und Erken—Görvälän andererseits in bezug auf Frischgewicht je Quadratmeter nicht so groß sind, wie wenn man das Frischgewicht je Kubikmeter betrachtet.

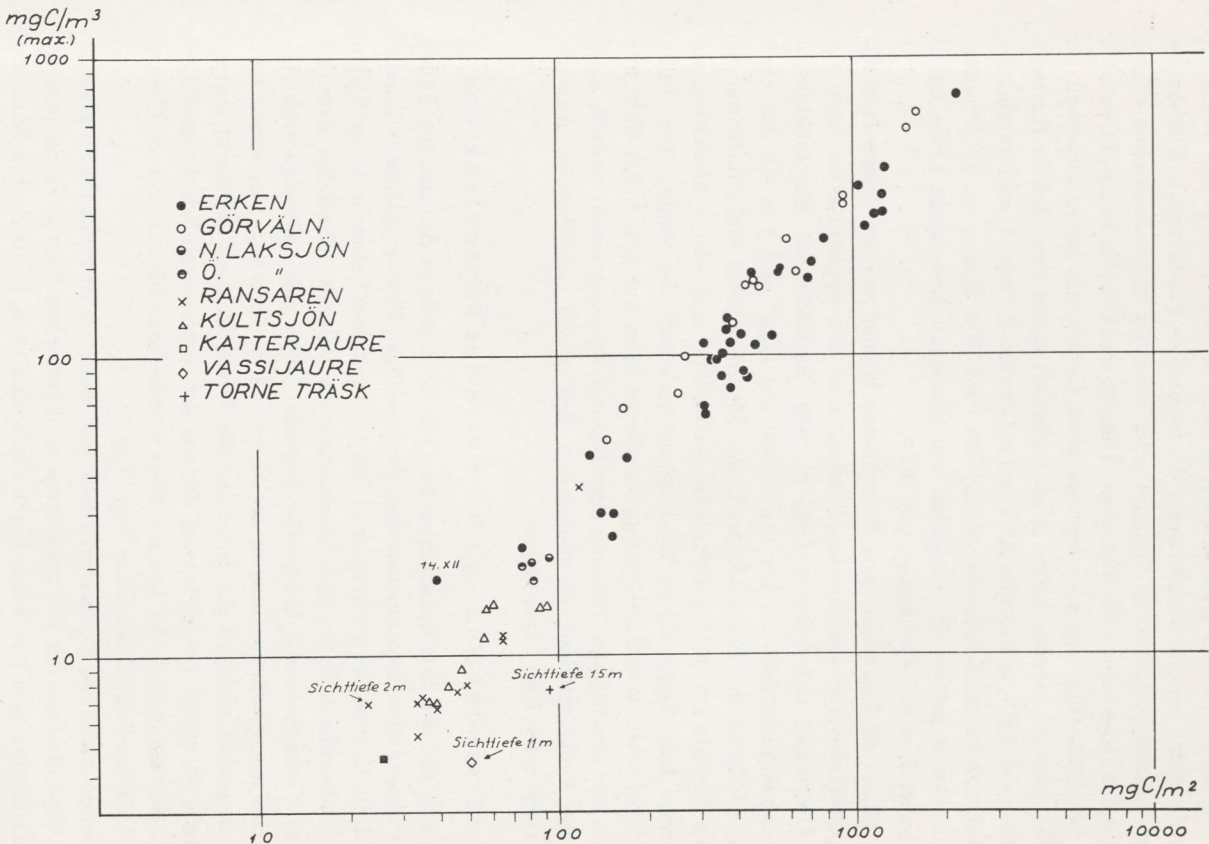


Fig. 8. Logarithmische Darstellung der Beziehung zwischen maximaler Primärproduktion je Volumeneinheit und gleichzeitiger Primärproduktion je Oberflächeinheit; das Diagramm umfaßt sämtliche hier benutzte C^{14} -Serien.

Hier sind wir aber besonders an der Relation zwischen Primärproduktion und Frischgewicht interessiert, und in Fig. 9 sind die Werte für diese Größen, beide berechnet je Volumeneinheit, in einem doppellogarithmischen Diagramm dargestellt. Die Streuung ist beträchtlich und beträgt in beiden Richtungen etwa eine Zehnerpotenz. Nicht nur in verschiedenen Seen, sondern auch im selben See kann

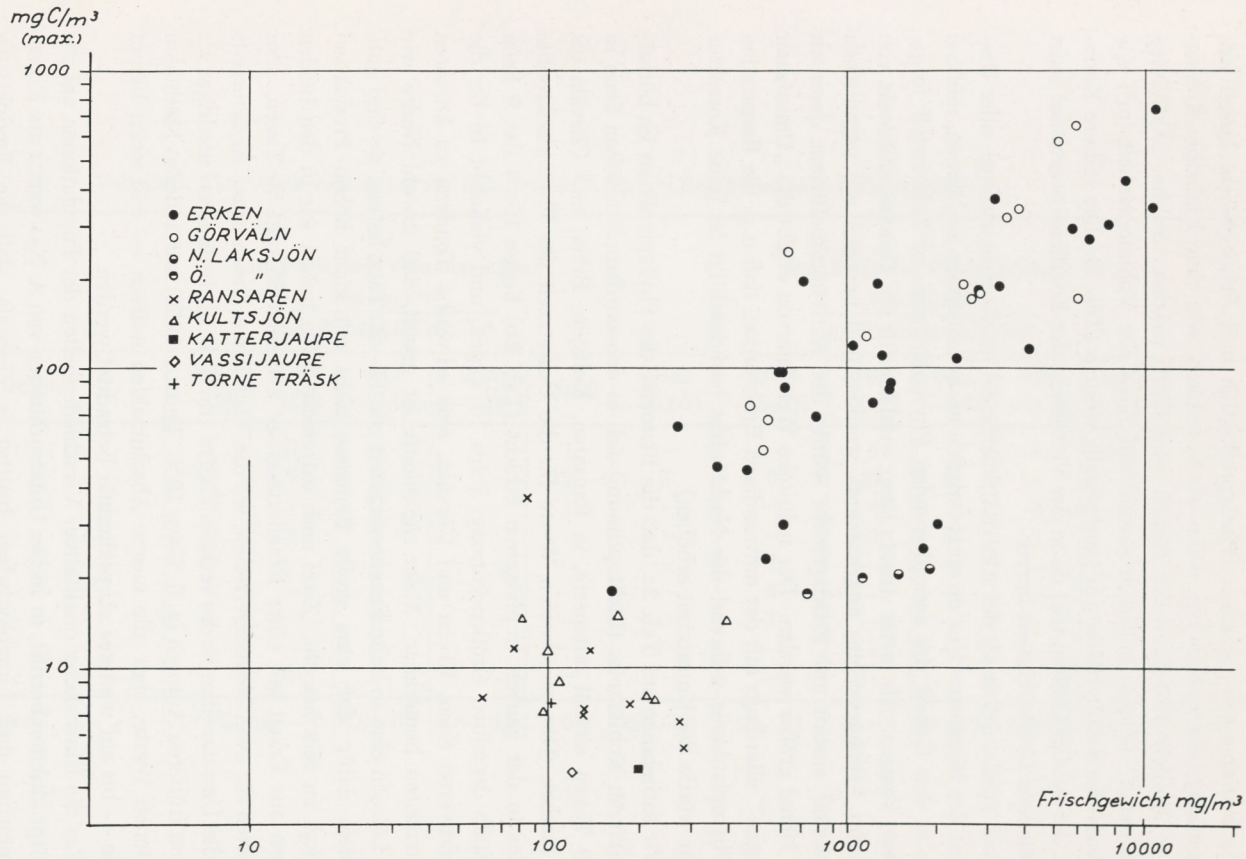


Fig. 9. Logarithmische Darstellung der Beziehung zwischen der täglichen Primärproduktion im lichtoptimalen Kubikmeter und der durchschnittlichen Biomasse des Phytoplanktons je Kubikmeter der trophogenen Schicht.

eine gewisse Biomasse eine recht variierende Produktion organischer Substanz je Tag aufzuzeigen, und umgekehrt kann eine gewisse Produktion von einer kleineren oder größeren Biomasse geleistet werden. Zu demselben Ergebnis wären wir gekommen, wenn wir statt Volumeneinheit die Flächeneinheit als Vergleichsbasis gewählt hätten.

Die Beziehungen zwischen Primärproduktion und Frischgewicht lassen sich zahlenmäßig besser studieren, wenn wir berechnen, wie viele Einheiten Kohlenstoff je Einheit Frischgewicht täglich assimiliert werden. Solche „Aktivitätskoeffizienten“ können natürlich sowohl auf Basis der Volumeneinheit (m^3) wie auf Basis der Seeoberfläche (m^2) aufgestellt werden (Tab. 2). Die lockere Korrelation der beiden Größen tritt da in der Verteilung der Koeffizientwerte auf recht verschiedene Größenklassen hervor.

Noch anschaulicher als der Aktivitätskoeffizient ist die Erneuerungs- oder Umsatzzeit der Biomasse. Um sie einigermaßen exakt feststellen zu können, müßten wir u. a. den Gehalt des assimilierenden Phytoplanktons an Kohlenstoff (organischem) kennen. Als erster Ansatz kann wohl hierfür ein Durchschnittswert von 10% des Frischgewichtes angenommen werden, und bezogen auf organischen Kohlenstoff anstatt auf Frischgewicht würde der Aktivitätskoeffizient demnach etwa 10mal größer werden. Der reziproke Wert hiervon ergibt die „Umsatzzeit in Tagen“, allerdings mit der notwendigen Reservation, daß u. a. die Respiration des Phytoplanktons während der Nacht nicht berücksichtigt ist (eine Korrektur hierfür würde die Umsatzzeit erhöhen).

Wir entnehmen aus Tab. 2a, daß die Biomasse des Phytoplanktons im höchstproduktiven Kubikmeter (Lichtoptimum) sich in den nordlappländischen Seen in 2—10 Tagen einmal erneuerte, in Ransaren, Kultsjön, Erken und Görvål oft noch rascher. Die berechneten Werte für die Umsatzzeit des Phytoplanktonbestandes in der ganzen trophogenen Schicht (Tab. 2b) liegen für 6 der 9 Seen innerhalb derselben Größenordnung, 2 bis 10 Tagen, und vielleicht ist für die produktiveren Seen, Erken und Görvål, eine schwache Tendenz zu kürzeren Umsatzzeiten bemerkbar. Mehr signifikativ ist gewiß, daß sowohl Nedre wie Övre Laksjön eine so hohe Erneuerungszeit wie 11—20 Tage haben; sie sind gute Beispiele dafür, daß eine große Biomasse nicht mit einer hohen Produktion identisch zu sein braucht. Zwei noch extremere Fälle haben wir in den beiden Werten aus Erken mit einer Erneuerungszeit zwischen 25 und 50 Tagen, aber sie gelten für zwei Novemberserien, wo die Tage schon kurz waren. Andererseits sind die Umsatzzeiten in der rechten Hälfte von Tab. 2b bedeutend niedriger als die von früheren Autoren (z. B. GRIM 1950, THOMAS 1950) mit anderen Methoden erhaltenen Werte, aber alle unsere Absolutzahlen müssen — wie schon betont wurde — bis auf weiteres als präliminär betrachtet werden.

Was die Einwirkung qualitativer Verschiedenheiten der Populationen auf die Primärproduktion betrifft, so zeigen Untersuchungen von A. NAUWERCK am Erkenlaboratorium und Limnologischen Institut in Uppsala, daß die Produktionsaktivität je Frischgewicht für verschiedene Planktonalgen sehr verschieden sein kann und daß in dieser Hinsicht vielleicht auch gewisse charakteristische Unterschiede bestehen zwischen größeren Algengruppen, wie z. B. Kieselalgen und Grünalgen. Wesentlich ist hier auch die Zellengröße, da kleinere Algen in der Regel effektivere Produzenten sind als größere (je Einheit Frischgewicht, gleicher

Tabelle 2. Aktivitätskoeffizienten für Frischgewicht, Anzahl Koeffizienten je Größenklasse.

Größe des Koeffizienten	a Auf Basis der Volumeneinheit mg C _{ass} /m ³ mg Frischgewicht/m ³					b Auf Basis der Flächeneinheit mg C _{ass} /m ² mg Frischgewicht/m ²						
	0,01 —0,05	0,06 —0,10	0,11 —0,15	0,16 —0,20	> 0,20	0,002 —0,004	0,005 —0,009	0,01 —0,02	0,03 —0,04	0,05 —0,06	0,07 —0,08	> 0,09
Görvåln	1	6	4	1	1	—	—	2	7	3	—	1
Erken	11	9	6	2	2	2	2	10	11	4	1	—
Ransaren	5	1	2	—	1	—	—	4	2	2	—	1
Kultsjön	3	3	1	1	—	—	—	3	3	1	1	—
Nedre Laksjön	2	—	—	—	—	—	2	—	—	—	—	—
Övre Laksjön	2	—	—	—	—	—	2	—	—	—	—	—
Katterjaure	1	—	—	—	—	—	1	—	—	—	—	—
Vassijaure	1	—	—	—	—	—	—	1	—	—	—	—
Torne träsk	—	1	—	—	—	—	—	—	1	—	—	—
„Umsatzzeit in Tagen“	10—2	1,7—1	0,9—0,7	0,6—0,5	< 0,5	50—25	20—11	10—5	3—2,5	2—1,6	1,4—1,2	< 1,1

Primärproduktion und Seetypen

Grad von Autotrophie vorausgesetzt). Die Bedeutung des Nannoplanktons ist somit sogar noch größer für die Primärproduktion als für die Biomasse des bestehenden Bestandes (vgl. RODHE, VOLLENWEIDER und NAUWERCK 1955).

Tabelle 3.

See	Erken		Görvåln		Ransaren		Kultsjön	
	1 m		1 m		1 m		1 m	
Tiefe								
Datum (1955)	8. 8.	22. 8.	8. 8.	22. 8.	11. 8.	22. 8.	12. 8.	22. 8.
Temperatur, °C	19,0	21,1	18,7	20,9	11,9	13,5	10,9	13,3
Leitfähigkeit, $\%_{20} \cdot 10^6$. . .	268	265	198	202	33,0	32,8	26,6	27,4
pH	8,2	8,7	8,0	8,0	7,5	7,3	7,3	7,3
Alkalinität, milliäquivalent/l	1,803	1,805	0,979	1,001	0,248	0,261	0,187	0,205
Gesamt-CO ₂ , mg/l	80,1	78,2	44,0	45,1	11,8	12,9	9,2	10,1
O ₂ , mg/l	8,8	10,7	8,6	8,7	10,7	10,1	10,2	10,0
NO ₃ -N, $\mu\text{g/l}$	0	0	104	128	10	9	14	10
PO ₄ -P, $\mu\text{g/l}$	2,1	0,9	2,2	4,2	—	0,5	—	0,6
Si, mg/l	0,93	0,82	0,81	0,69	0,77	0,75	0,78	0,79
Primärproduktion, mg C/m ³	96	425	73	72	37	11	11	9
Frischgewicht, mg/m ³	664	8681	762	470	85	138	101	86
Aktivitätskoeffizienten für Frischgewicht	0,15	0,05	0,10	0,16	0,43	0,08	0,11	0,10

Wie die näheren Beziehungen zwischen Primärproduktion und stofflichen Bedingungen verlaufen, ist noch so unklar, daß hierüber kaum etwas sicheres zu sagen ist. In Tab. 3 sind für die vier am besten bekannten Seen (zwei in Uppland, zwei in Lappland) einige Daten für 1 m Tiefe aus je zwei Untersuchungsreihen zusammengestellt. In Erken war der Nitratgehalt im Epilimnion den ganzen August durch praktisch genommen null und der Phosphatgehalt meistens geringer als 2 $\mu\text{g P/l}$, aber trotzdem erreichte die Produktion dort weit höhere Werte als in Görvåln, wo der Nitratstickstoff nicht 100 $\mu\text{g/l}$ und der Phosphatphosphor nicht 2 $\mu\text{g/l}$ unterschritten. Die beiden Lapplandseen hatten auch mehr Nitrat und nicht viel weniger Phosphat als Erken, aber dennoch war ihre maximale Primärproduktion je Kubikmeter etwa 10mal kleiner. Je Frischgewicht gerechnet (Aktivitätskoeffizienten) lag aber die Produktionsleistung in allen vier Seen innerhalb ungefähr derselben Größenordnung, mit Ausnahme eines sehr hohen Wertes (0,43) in Ransaren, der recht zweifelhaft erscheint.

Wären die Konzentrationen der beiden klassischen Minimumstoffe, Phosphat und Nitrat, allein oder hauptsächlich allein ausschlaggebend für die quantitative Entwicklung des Phytoplanktons, dann würde es kaum verständlich sein, daß so große Unterschiede in Phytoplanktonbiomasse und Primärproduktion, wie die Beispiele für hoch- bzw. geringproduktive Seen in Tab. 3 aufweisen, zustandekommen können. Vorläufige C¹⁴-Versuche mit verschiedenen Zusätzen haben mich überzeugt, daß organische Stoffe, die im Hypolimnionwasser nahrungsreicher Seen vorkommen, oft eine viel größere Beschleunigung der Produktion hervor-

rufen als Zugaben von Phosphat und Nitrat. Man kann sich gut vorstellen, daß organische Stoffe wie Vitamine (z. B. B₁₂) bei der bakteriellen Zersetzung des absterbenden oder abgestorbenen Planktons gebildet werden und dann bei der Einmischung von Tiefenwasser in die trophogene Schicht die Produktion neuer organischer Substanz kräftig begünstigen, also sozusagen wie Autokatalysatoren wirken. Eine Voraussetzung für weitere Produktionssteigerung ist zwar, daß Phosphor und Stickstoff in hinreichenden Mengen zur Verfügung stehen oder früher in den Zellen in Überschuß angereichert wurden. Der P- und N-Bedarf vieler Algen ist aber — aus dem Gesichtspunkt des analytischen Chemikers — äußerst gering, und außer den momentanen Konzentrationen sollten auch die Regenerationsgeschwindigkeiten der Nährstoffe berücksichtigt werden (wozu aber noch adequate Methoden fehlen). Es ist demnach nicht verwunderlich, daß die Relation der Primärproduktion zu den feststellbaren Phosphat- und Nitratgehalten keineswegs eindeutig ist.

Die Effektivität der Primärproduktion

Als „Produktionsgröße“ definiert KALLE (1948) den Anteil der im Laufe eines Jahres von der Sonne dem Biotop zugestrahlten Energie, der, anstatt sogleich in Wärme oder Bewegungsenergie überzugehen, den Umweg über die Reduktion der Kohlensäure zu organischer Substanz einschlägt. Es wäre gewiß ein großer Fortschritt, wenn wir an Hand ihrer Produktionsgrößen verschiedene Seen direkt miteinander und mit dem Meer vergleichen könnten, aber bisweilen verfügen wir nur über einige wenige Daten (vgl. die Zusammenstellung bei VOLLENWEIDER 1956). Für Erken sind jedoch genug zahlreiche C¹⁴-Versuche in allen Jahreszeiten durchgeführt worden, um die Berechnung der Ausnützung der einstrahlenden Energie während eines Jahres zu gestatten.

Zu diesem Zweck wurde die Primärproduktion je Quadratmeter (mg C/m²) in gcal/cm² umgerechnet und — der Übersichtlichkeit halber — dekadentweise summiert (gemäß linearer Interpolation zwischen konsekutiven Werten). Ebenso wurden die Meßwerte der einstrahlenden Gesamtenergie behandelt. In Fig. 10 sind oben die beiden Histogramme für die Zeitspanne vom 1. Oktober 1953 bis 30. August 1955 gegeben, wobei die Skala für die Einstrahlung zur Erleichterung des Vergleiches 1000mal kleiner gewählt ist. Bei einer Effektivität von 0,1⁰/₀ sind somit die Stapeln beider Histogramme gleich hoch. Im unteren Teil des Diagrammes ist die Effektivität direkt angegeben.

Wir sehen, daß die Effektivität recht großen jahreszeitlichen Schwankungen unterlegen ist. Die niedrigsten Werte von etwa 0,1⁰/₀₀ finden wir erwartungsgemäß unter dem Eis; eine Korrektur für die Abschirmung des Lichtes durch die Eis- und (besonders!) Schneedecke würde jedoch ergeben, daß die Ausnützung der wirklich in das Wasser eindringenden Energie doch nicht viel geringer ist als im Sommer. Denn nicht im Sommer, sondern im Frühjahr und Herbst werden die

Höchstwerte der Effektivität erreicht, ja, den allerhöchsten Wert zeigte die Effektivität sogar spät im Dezember (1953), wo zwar die Produktion absolut gesehen gering war, aber im Verhältnis zur einstrahlenden Energie doch einen beträchtlichen Anteil (6,6‰) ausmachte.

Das Sommerminimum der Effektivität ist wohl hauptsächlich durch die Erschöpfung der Nährstoffvorräte während des Frühjahrsmaximums bedingt. Im August und in den folgenden Monaten ist die Effektivität höher, aber dann macht sich die abnehmende Tageslänge schon in einer kontinuierlichen Abnahme der Absolutproduktion bemerkbar, d. h., der Lichtfaktor wirkt begrenzend. Nur im Frühjahr sind sowohl die stofflichen Produktionsbedingungen wie das Licht zugleich maximal günstig, und der See leistet dann sein Äußerstes.

In Erken beginnt der Anstieg der Frühjahrsentfaltung ungefähr Anfang April, wenn das Licht beim Abschmelzen des Schnees auf dem Eis immer besser ins Wasser eindringen kann, und der Höhepunkt des Maximums kann fast schon vor dem Eisbruch, Ende April oder Anfang Mai, erreicht werden. Sowohl die Höhe dieses Gipfels wie seine zeitliche Ausdehnung scheint von Jahr zu Jahr zu wechseln: Im Jahre 1954 wurden die Höchstwerte, etwa 1200 mg C/m²/Tag, für eine Periode von 8 bis 10 Tagen verzeichnet, wogegen 1955 ein viel höherer Gipfel, 2200 mg C/m²/Tag, erreicht wurde, aber dann nur einige wenige Tage bestand (diese Unterschiede in der täglichen Produktion sind in der Dekadendarstellung von Fig. 10 nicht ersichtlich). Später im Mai wird die Tagesproduktion immer geringer, und am Ende des Monats kann die Frühjahrsentfaltung als abgeschlossen angesehen werden (vgl. Fig. 10).

Berechnen wir die gesamte Produktionsleistung während dieser Periode, also von Anfang April bis Ende Mai, so ergibt sich für Erken eine überraschende Konstanz von Jahr zu Jahr (Tabelle 4). Wenigstens für diesen See, der nach einer mehrmonatigen Ruhepause unter dem schneebedeckten Eis regelmäßig eine mächtige Frühjahrsproduktion aufzeigt, scheint deshalb die Behauptung berechtigt, daß die gesamte Neubildung organischer Substanz während der Frühjahrsentfaltung als ein repräsentativer Ausdruck der maximalen Leistungsfähigkeit des Sees betrachtet werden kann. Sollte dies eine Regel sein, die auch für andere Seen mit ausgesprochenen Frühjahrsmaxima Geltung hat, dann ist uns hier eine Vergleichsbasis gegeben, die regional anwendbar ist.

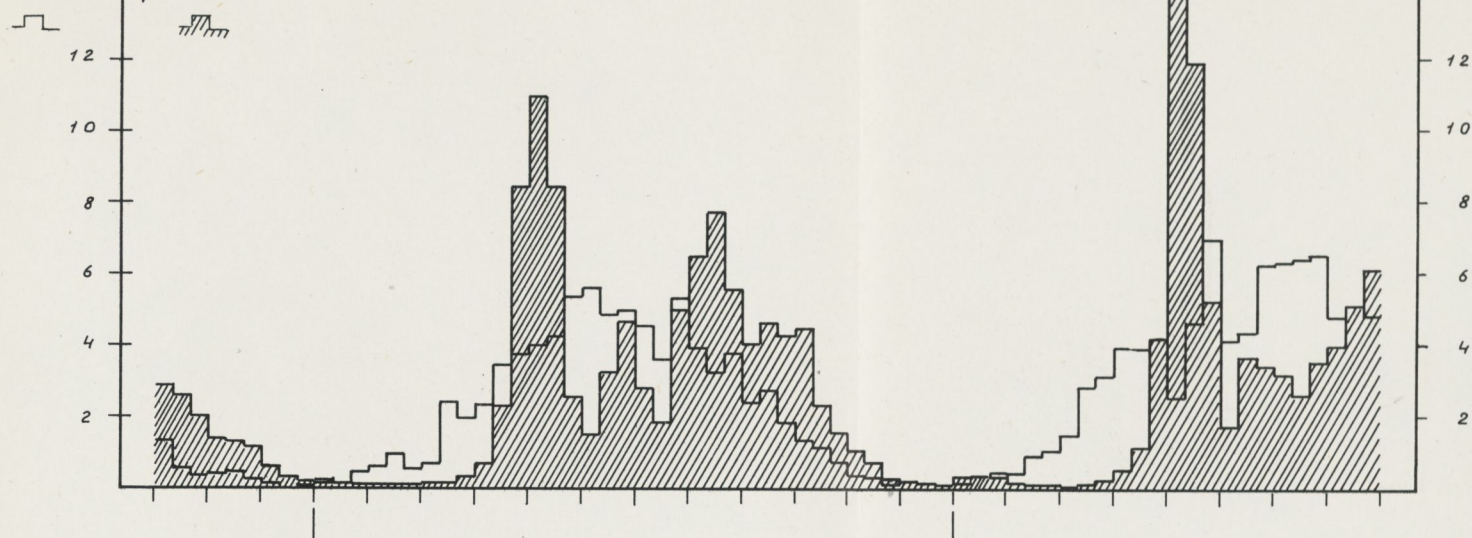
Tabelle 4.

Jahr	1. April—31. Mai			Effektivität ‰
	Gesamte Primärproduktion		Gesamte Einstrahlung gcal/cm ²	
	mg C/m ²	= gcal/cm ²		
1954	35 400	33,3	23 200	1,44
1955	39 200	36,8	26 200	1,40
1956	37 300	35,0	26 500	1,39

ERKEN

Einstrahlung
 10^3gcal/cm^2
 pro Dekade

Produktion
 gcal/cm^2
 pro Dekade



Effektivität

‰

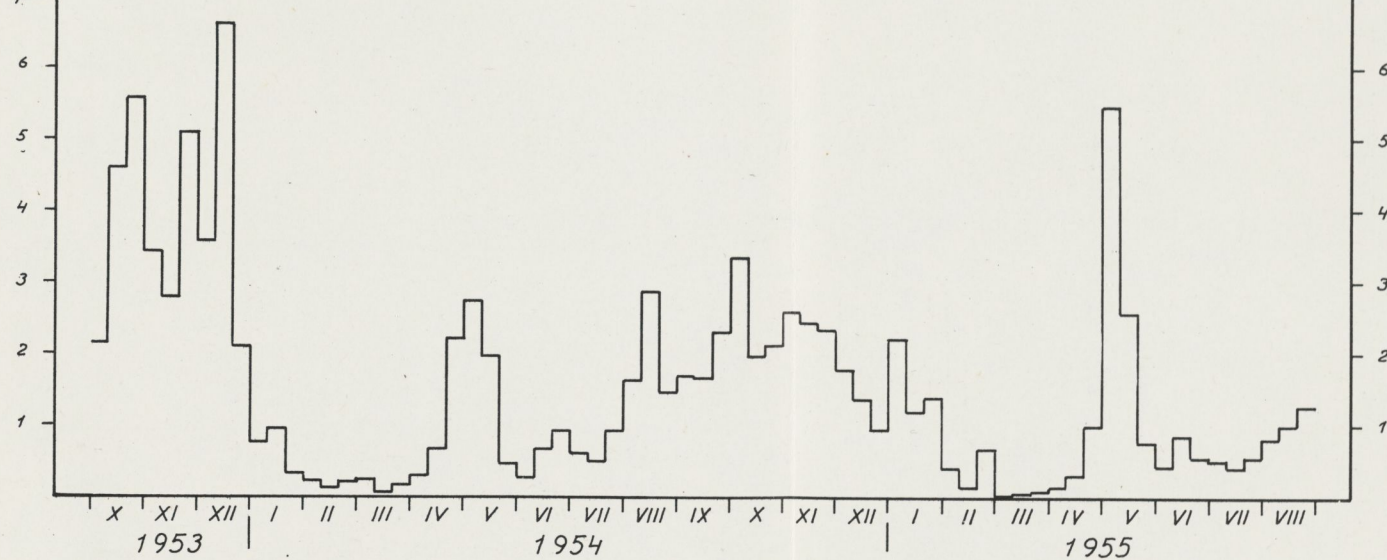
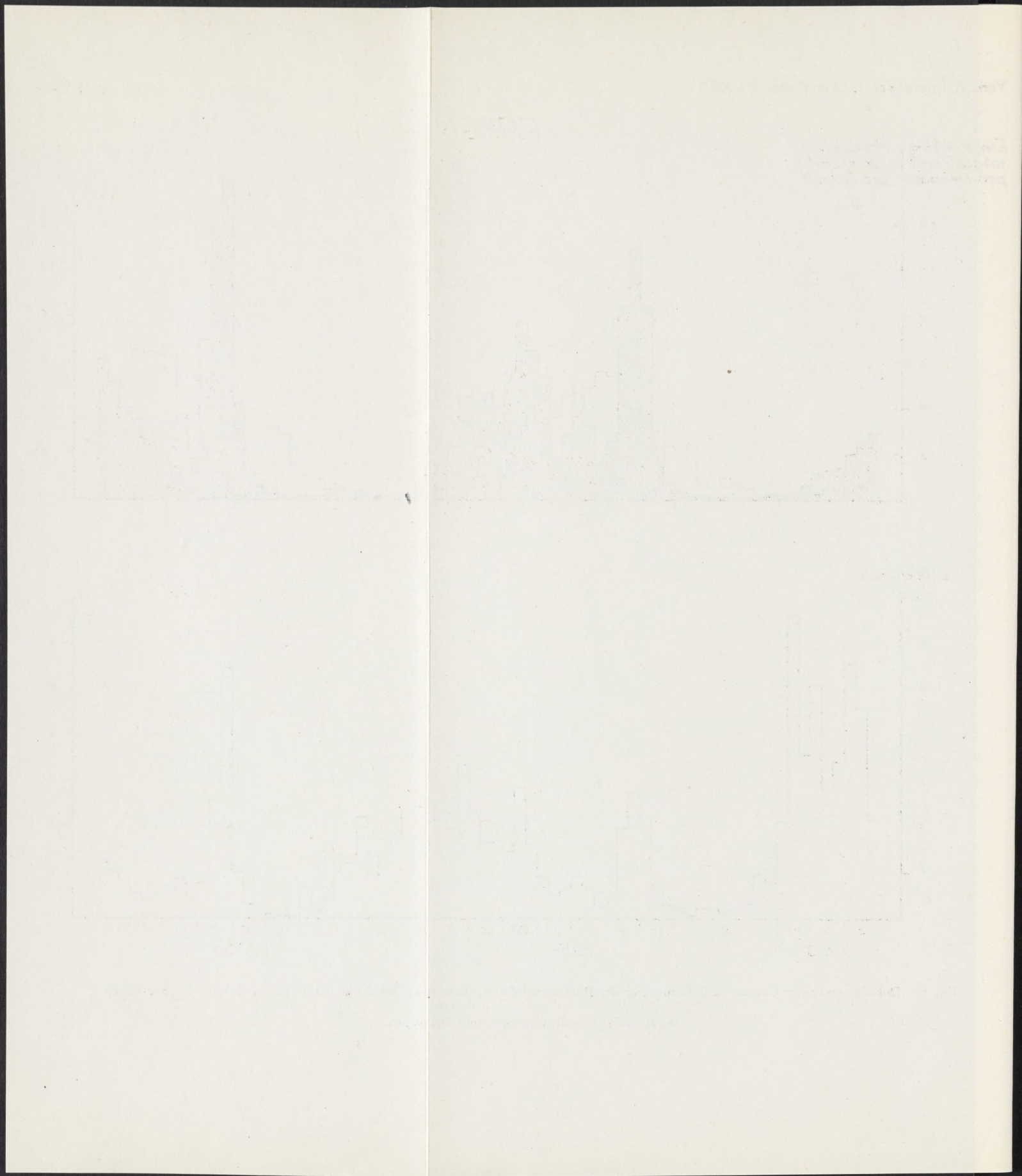


Fig. 10. Dekadenwerte der Gesamteinstrahlung und der Primärproduktion sowie der Effektivität der Primärproduktion im See Erken.

W. Rodhe: Primärproduktion und Seentypen.



Für das Jahr 1954 ist die KALLE'sche Produktionsgröße mit Hilfe der in Fig. 10 dargestellten Daten leicht zu berechnen. Die gesamte Einstrahlung betrug in diesem Jahr 82 910 gcal/cm², die Primärproduktion 104 000 mg C/m² = 97,73 gcal/cm². Die Produktionsgröße Erkens war also im Jahre 1954 $97,73/82,91 = 1,2^0/00$.

Hierzu muß allerdings wieder der Vorbehalt gemacht werden, daß die berechnete Produktionsgröße strenggenommen nicht für den See als Ganzheit, sondern nur für die benutzte Station im östlichen Teil gültig ist und daß, zweitens, auch die physiologisch-ökologische Signifikanz der absoluten Produktionswerte näher aufgeklärt werden muß.

Seetypen und Primärproduktion

Nachdem ich nun diese Daten für die Primärproduktion einiger Seen vorgelegt habe, möchte ich versuchen, folgende Frage zu beantworten: Wie kann die nunmehr mögliche Bestimmung der Primärproduktion für eine quantitative Feststellung der biologischen Seetypen ausgenützt werden?

Zuerst muß ich da, um Mißverständnisse zu vermeiden, eine Binsenweisheit bringen: Das biologische Geschehen in den Seen ist viel zu kompliziert, um jemals in einem einzigen Wert oder Index gefaßt werden zu können. Die Primärproduktion, so wichtig sie auch ist, stellt nur einen Aspekt dar, und in dem Kreislauf der Stoffe sind, wie z. B. OHLE (1955) neulich hervorgehoben hat, der Umbau (= Sekundärproduktionen) und der Abbau (= Mineralisation) der organischen Substanz ebenso vital für den See wie der Aufbau. Von ebenbürtiger Bedeutung sind die Produktionsbedingungen chemischer und physikalischer Art und die in ihnen sich auswirkende Morphometrie des Sees. Wenn wir die Eigenart eines Sees hinreichend kennzeichnen wollen, müssen wir also — ebenso wie bei der Kennzeichnung eines Organismus — eine ganze Reihe von Merkmalen heranziehen. Aber wie die Beschreibung eines Individuums umfassender und mehr detailliert ist als die Feststellung seiner Artcharaktere, sollte die Vielfältigkeit der Eigenschaften der einzelnen Seen nicht ein einfaches System der Seetypen ausschließen.

Es handelt sich also darum, eine einheitliche Basis zu finden, die sowohl theoretisch begründet wie praktisch meßbar als gemeinsamer Nenner für die Seetypen dienen kann. Diese Aufgabe ist noch immer der heiße Brei, um den die Limnologen seit mehr als drei Jahrzehnten kreisen! Soll der Trophiebegriff nicht vollständig verworren und dadurch unbrauchbar werden, muß seine Definition nun endlich einheitlich festgelegt werden. Hierzu muß man zunächst entscheiden, ob die Produktionsbedingungen oder die Produktion selbst als das eigentliche Kriterium der Trophie benutzt werden soll. Daß nicht beide Aspekte auf einen gemeinsamen Nenner gebracht werden können, zeigt die bisherige Entwicklung der Seetypenlehre zur Genüge.

Besonders klar wird das Dilemma in einer kürzlich erschienenen Arbeit von FINDENEKG (1955) beleuchtet. Er befürwortet eine grundsätzliche Trennung des

Trophiebegriffes von der Produktion und schlägt vor, als „Trophiezustand“ einzig und allein die stoffliche Grundlage der Organismen zu betrachten. Nach FINDENEGG sollte auch bei der Benennung von Seetypen „der Stamm . . . troph‘ nur dann Anwendung finden, wenn er sich wirklich nur auf die ernährungsphysiologische Beschaffenheit des Wassers bezieht . . .“ (S. 95). Er hat aber selbst Schwierigkeiten, diese strikte Linie konsequent zu halten, wenn er z. B. schreibt (S. 91), daß ein eutropher See „zuzeiten erkennbar sein (wird) an der hohen Konzentration der Nährsalze, in anderen Fällen an der großen Planktondichte“, und daß es gleichgültig ist, ob die ernährungsphysiologische Beschaffenheit des Wassers „aus chemischen, optischen oder planktischen Untersuchungen abgeleitet wird“ (S. 95). Wie finden wir aber dann die einheitliche, meßbare Basis der Trophie, die wir unbedingt brauchen, um — mit FINDENEGG's Worten (S. 92) — „dem Ziele . . ., diese Trophie möglichst exakt, das heißt zahlenmäßig, abzustufen“, näher zu kommen?

Eine solche zahlenmäßige Abstufung der Trophie können wir dagegen erzielen, wenn der Trophiebegriff ganz mit der Primärproduktion des freien Wassers verknüpft wird. Dies würde sich recht gut mit der ursprünglichen Auffassung von NAUMANN (1917) decken, nur daß er damals keine praktische Möglichkeit hatte, die Primärproduktion direkt zu messen und deshalb die Quantität des Phytoplanktons als maßgebende Eigenschaft benutzte, um die Resultante der gesamten Produktionsbedingungen im See zu beurteilen. Da durchschnittlich eine gewisse Korrelation zwischen Planktondichte und Planktonproduktion besteht (vgl. Fig. 9), würde eine konsequente Bezugnahme auf die dynamische anstatt der statischen Größe keine große Veränderung in der Typenklassifizierung der meisten bisher als oligotroph bzw. eutroph bezeichneten Seen mit sich führen, sie würde aber eine zahlenmäßige Feststellung ihrer Lagen in der Trophieskala ermöglichen.

Wenn wir unter diesem Gesichtspunkt die Produktionswerte je Oberflächen- und Volumeneinheit des soeben vorgelegten Materials wieder betrachten (Fig. 8), sehen wir, daß die Tagesraten in den beiden gewiß eutrophen Seen Erken und Görvåln fast jederzeit (einzige Ausnahme ist ein Wert für Erken am 14. Dezember) bedeutend höher liegen als diejenigen der oligotrophen Lapplandseen. Es wäre verlockend, eine scheidende Grenze zwischen Oligotrophie und Eutrophie bei etwa $100 \text{ mg C/m}^2 \cdot \text{Tag}$ bzw. $25 \text{ mg C/m}^3 \cdot \text{Tag}$, max. zu ziehen, aber teils ist das Material noch zu klein für eine solche generelle Aussage, teils sollte man überhaupt mit Grenzl意思ien, die in der Natur kaum bestehen, vorsichtig umgehen.

Auf Grund der großen jahreszeitlichen Schwankungen der Einzelwerte ist es schwer, an Hand von einzelnen Bestimmungen einen See auf einem gewissen Platz in einer Skala für Tagesproduktionen einzuordnen. Zu diesem Zweck scheint es besser, eine entsprechende Skala für die gesamte Jahresproduktion je Flächeneinheit zu benutzen. Für Erken betrug die Primärproduktion im Jahre 1954 ins-

gesamt etwa 104 g C/m^2 , und es würde gewiß von großem Interesse sein, auf dieser Basis analoge Werte aus verschiedenen Seen (nicht zuletzt Seen aus anderen Breiten!) miteinander vergleichen zu können. Wäre dann der Trophiegrad identifiziert mit der Primärproduktion, so würden wir direkt und zahlenmäßig den Trophiegrad der Seen auf der Skala projiziert erhalten.

Als eine logische Konsequenz aus diesen Überlegungen folgt, daß das ganze Trophiesystem äußerst vereinfacht wird, indem nur die beiden Haupttypen „oligotroph“ und „eutroph“ gemäß der Verknüpfung des Trophiebegriffes mit der Primärproduktion mit dem Stamm „... troph“ bezeichnet werden. Alle übrigen ehemaligen „Trophien“ — wie Dystrophie, Mixotrophie, Azidotrophie, Argillotrophie und Siderotrophie — sollten verschwinden oder, falls nötig, umgetauft werden. Im Grunde genommen erscheinen sie alle ziemlich überflüssig, da sie durch einfache Adjektive ersetzt werden können (z. B. humose oligotrophe oder eutrophe Seen anstatt dystrophe bzw. mixotrophe Seen, schwefelsaure Seen anstatt azidotrophe, lehmgetrübte anstatt argillotrophe und seerzführende anstatt siderotrophe Seen).

Wünscht man die Relationen der einen oder anderen Eigenschaft zu verschiedenen Trophiegraden zu studieren, so eignet sich die Oligotrophie-Eutrophie-Skala gewiß als Abszisse in Diagrammen, wo die betreffende Eigenschaft auf der Ordinate eingetragen wird. Desgleichen könnte man, soweit numerische Daten zur Verfügung stehen, die Sekundärproduktionen, die Produktion des Litorals und die des Profundals sowie andere wichtige Charaktere auf einer Ordinate der Trophieachse gegenüberstellen. Auch Eigenschaften qualitativer Art, wie die Zusammensetzung des Planktons oder der Bodenfauna, würden für verschiedene Seen gewiß besser vergleichbar werden, falls sie konsequent auf eine einheitliche Trophieskala bezogen wären.

Es mag erscheinen, daß ich hier die Bedeutung der Primärproduktion im Verhältnis zu allen anderen wichtigen Aspekten der Seetypenfragen kräftig übertrieben habe. Ich bilde mir nicht ein, daß der Aufbau der organischen Substanz im Leben der Seen wichtiger ist als der Umbau und der Abbau, bin aber überzeugt, daß nur die Primärproduktion uns eine einheitliche Basis zum vergleichenden Studium des Stoffwechsels verschiedener Seen geben kann. Deshalb sollte nach meiner Meinung die Primärproduktion auch die Basis der biologischen Seetypen sein.

Für überaus wertvolle Mitarbeit möchte ich schließlich besonders folgenden Personen meinen besten Dank aussprechen: Fräulein ANNA PANDERS für ihre aufopfernde Arbeit mit der C^{14} -Technik, Herrn ARNOLD NAUWERCK für Daten aus seinen Phytoplanktonzählungen, Amanuens LARS KARLGREN und Ingenieur ÅKE SIKSTRÖM für chemische Analysen, Fil. mag. BÖRJE LARSSON mit Frau INGA-LIS für C^{14} -Serien und Probenentnahmen in Ransaren-Kultsjön, Ingenieur VILHELM NILSSON für desgleichen in Görvåln und Dr. R. A. VOLLENWEIDER für anregende Diskussionen und wertvolle Kritik.

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Summary

Primary production and lake typology

In 2 high-productive lakes in southern Sweden (Uppland: Erken and Görväln) and 7 low-productive lakes in northern Sweden (Lappland: Ransaren, Kultsjön, Nedre [= Lower] Laksjön, Övre [= Upper] Laksjön, Katterjaure, Vassijaure, and Torne träsk), the primary production of organic matter by phytoplankton has been measured *in situ* with the C^{14} -technique introduced by STEEMANN NIELSEN. From curves for the vertical distribution of the daily production (figs. 1 and 2), the production rate has been calculated for each cubic meter of the trophogenic

stratum ($\text{mg C}_{\text{ass}}/\text{m}^3$), for the cubic meter in which the light conditions are optimal ($\text{mg C}_{\text{ass}}/\text{m}^3$, max.), and for the whole trophogenic layer ($\text{mg C}_{\text{ass}}/\text{m}^2$). The ratio between the two latter values (cfr. table 1) is mainly dependent upon the optical conditions in the water and roughly related to the transparency (figs. 3—7). The absolute values of the daily production during the ice-free season (fig. 8) are considerably higher in Erken and Görvältn (between about 100—2200 $\text{mg C}/\text{m}^2$ and 25—750 $\text{mg C}/\text{m}^3$, max.) than in the lakes in Lappland ($< 100 \text{ mg C}/\text{m}^2$ and $< 25 \text{ mg C}/\text{m}^3$, max.).

While the relationship between daily production rates and corresponding values for the standing crop (fresh weight) of phytoplankton varies within a wide range, the data indicate that in general a proportionate relation does exist between them (fig. 9). The daily production per unit fresh weight — a quotient indicating the productive activity of the total phytoplankton — has an approximately similar range of variation in all the lakes investigated (table 2). Preliminary values for the turn-over time vary between 0.5 and 10 days for the optimal light layer, and between 1 and 50 days for the trophogenic zone as a whole. A slight tendency towards higher activities may be significant for the high-productive lakes in Uppland. Their epilimnic concentrations of phosphate-phosphorus and nitrate-nitrogen, however, may be as low or even lower than the contents in the Lappland lakes (table 3).

For Lake Erken the efficiency of the primary production in relation to the incident radiation has been calculated for a period of 23 months (fig. 10). The decade (10-day) values from different seasons vary between about 0,01% and 0,6% (extreme single-day values are more apart) and for the whole year 1954, when a total of 104 000 mg organic carbon was produced per m^2 , the efficiency of the lake was found to be 0,12%. The amount of organic carbon produced by the spring maximum (during about 2 months, beginning almost a month before the breaking up of the ice) proved to be nearly constant (about 37 000 $\text{mg C}/\text{m}^2$) in the years 1954, 1955, and 1956 (table 4). If this constancy is significant, the value can be used as a measure of how much the lake can produce when it is at its best.

Some basic concepts of lake typology are shortly discussed. It is claimed that the serious confusion characterizing present use of the "... trophic" terms is due mainly to the fact that the trophic system still lacks a uniform and quantitatively measurable basis. It is impossible to establish such a basis, if both the conditions of organic production and this production itself (or the standing crop) are selected as criteria for trophic types. We have to decide, upon which aspect of lake metabolism these types are to be founded.

Since only the primary production seems able to offer a uniform, quantitative basis — theoretically correct as well as practically useful — for the trophic system, it is suggested that all "... trophic" lake types except oligotrophic and eutrophic be abandoned and the rate of primary production be used as the measure of the

degree of oligotrophy or eutrophy. Other characteristics of lakes (such as their chemical and physical conditions, morphometry, secondary production, as well as qualitative characters) may conveniently be compared and defined for various lakes, if plotted against the trophic axis as abscissa.

Diskussion

FINDENEGG: Es freut mich, feststellen zu können, daß RODHE mit meiner Auffassung über den Trophiebegriff sich insofern identifiziert, als auch er nur das als Trophie anerkennt, was sich direkt auf die Entstehung pflanzlicher Biomasse durch photosynthetische Prozesse bezieht, also alle „Trophien“ ablehnt, die nicht auf einer Skala zwischen Oligo- und Eutrophie liegen. Hinsichtlich der von mir vorgeschlagenen Definition, was unter Trophiezustand verstanden werden sollte, muß ich bemerken, daß zwischen der von mir vertretenen statischen Auffassung des Trophiebegriffes und der dynamischen von RODHE vielleicht kein so krasser Gegensatz besteht als es der Fall zu sein scheint. Ich halte meine Definition für logisch fundiert und praktisch anwendbar, gebe aber zu, daß sie einer zahlenmäßigen Einstufung in eine Skala Schwierigkeiten bietet. Sollte es sich herausstellen, daß RODHE's Auffassung eine exaktere Einstufung eines Sees möglich macht, so würde ich nicht zögern, mich ihr anzuschließen. Der Beweis hierfür muß allerdings erst erbracht und die Brauchbarkeit der Charakterisierung der Trophie durch die Primärproduktion erst erprobt werden.

RODHE: Der Gegensatz zwischen einer statischen und einer dynamischen Auffassung des Trophiebegriffes ist prinzipieller Art und als solcher ebenso klar wie scharf. Praktisch kann der Unterschied weniger schroff sein, was z. B. daraus hervorgeht, daß der Bestand und die Produktion des Phytoplanktons sich durchschnittlich ziemlich gleichartig verhalten. Deshalb ist die Zugrundelegung der Primärproduktion mehr übereinstimmend mit der ursprünglichen NAUMANN'schen Definition des Trophiebegriffes als FINDENEGG's Vorschlag, die Trophie als einen Zustand, und zwar als die durchschnittliche Konzentration der trophogenen Schichten an Nahrungsstoffen, zu definieren.

STANGENBERG: Ich möchte fragen, ob der Verfasser irgendwelche Angaben machen kann, in welcher Beziehung die Tierproduktion bzw. die Fischproduktion zur Primärproduktion steht, mit anderen Worten, ob man aus dem Eutrophie- oder Oligotrophiebegriff auf die Fischproduktion schließen kann.

RODHE: Es liegen noch zu wenige C^{14} -Bestimmungen aus verschiedenen Seen vor, um diese an und für sich alte Frage an Hand neuer Ergebnisse zu beantworten. Anzunehmen ist aber, daß die Beziehungen zwischen der Primärproduktion einerseits und den Sekundärproduktionen andererseits recht verschiedenartig sein können, da letztere nicht nur von der Produktion des Phytoplanktons, sondern zugleich von vielen anderen Faktoren abhängig sind. Es ist eine dringende und zugleich lockende Aufgabe, diese dynamischen Beziehungen mit den modernen Isotopmethoden näher zu studieren.

STEINBÖCK: Wie beim Vortrag ELSTER (siehe Diskussionsbemerkung daseibst) ist auch hier mit Nachdruck darauf hinzuweisen, daß die Primärproduktion allein in den „allotrophen“ (bisher „kryoeutrophen“) Seen ein gänzlich falsches Bild ergibt, da das „Empneuston“ — die wesentliche stoffliche Grundlage der Ernährung solcher Seen — nicht erfaßt ist.

RODHE: Das Bild wäre gewiß falsch, wenn man behaupten würde, daß nur die Primärproduktion einen See mit organischer Substanz versorgen kann. Die Eigenart der „kryoeutrophen“ Seen würde aber sicher noch besser zutage treten, wenn man ihre allotrophe Zufuhr durch das „Empneuston“ direkt mit ihrer autotrophen Primärproduktion vergleichen könnte (z. B. in einem Diagramm mit der allotrophen Versorgung auf der Ordinate, der autotrophen auf der Abszisse).

THOMAS: Die wertvollen Untersuchungsergebnisse von Dr. RODHE haben uns interessiert, weil sie manche Parallelitäten mit dem Sedimentationsvorgang erkennen lassen, wie er mit der Methode der Sedimentmeßpfanne dargestellt wurde. Ich frage mich jedoch, ob es nicht verfrüht ist, diese Ergebnisse vor einer weiteren Tiefen- und Breitenentwicklung der Methodik für die Seetypeneinteilung zu verwenden.

RODHE: Es wird sich zweifellos in wenigen Jahren zeigen, ob die Ergebnisse der C^{14} -Methode sich zur quantitativen Charakterisierung der Trophiestufen eignen oder nicht. Zur Zeit erscheint es mir wichtiger, mehr von solchen Ergebnissen aus verschiedenen Seen zu bringen als über terminologische Fragen zu streiten.

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THE PLANKTON OF NORTH TWIN LAKE, WITH
PARTICULAR REFERENCE TO THE SUMMER OF 1955¹

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INTRODUCTION

North Twin Lake is a shallow prairie lake in the north central portion of agriculturally-rich Calhoun County, Iowa. In 1939 and 1940 the lake was dredged by the Iowa State Conservation Commission to increase its recreational values. When the water flows over the barrier at the outlet into South Twin Lake, the 135 acre dredged portion of the lake is now 13 to 15 feet deep while the undredged northern portion has a maximum depth of 6 to 8 feet. The lake is approximately 2.5 miles long, northeast-southwest, and has a maximum area of 569 acres. During recent drought years the water level has fallen almost 3 feet below the outlet.

Higher aquatic vegetation both submersed and emergent is noticeably sparse and exhibits a somewhat spotty distribution in North Twin Lake. Emergent vegetation is present only in small amounts and in scattered locations around the lake proper. Only three forms were found to be prevalent. They included the cattail, Typha latifolia L.; the soft-stem bulrush, Scirpus validus Vahl.; and the river bulrush, Scirpus fluviatilis (Torr.) Gray. Potamogeton filiformis Pers. was the only submersed form detected and it occurred sparsely at several locations. Its annual development in most years appeared to follow a pattern of relatively luxuriant growth during the spring and early summer months followed by a rapid deterioration probably caused by progressive increases in water turbidity.

Attached filamentous algae occasionally attained good development in the shallows at the water's edge. The principal forms here were species of Cladophora and Stigeoclonium.

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²Now Fisheries Biologist, California Fish and Game Department, Stanford University, Palo Alto, Calif. The author wishes to express his appreciation to Dr. K. D. Carlander for encouragement and guidance throughout the study, to Drs. J. D. Dodd, W. T. Edmonson, E. R. Becker, M. J. Ulmer, and G. W. Prescott for aid in identifying various plankton organisms, and to Dr. Dodd for loan of photographic equipment and assistance in taking pictures of various organisms. Valuable field assistance was given by Dr. J. B. Owen and M. Tagatz. The author's wife, Bobbie Jean, gave continuous encouragement and much help in tabulations and in field work.

North Twin Lake is quite shallow and is subjected to almost continual wind activity, since the surrounding countryside provides little shelter. As a result, definite permanent thermal stratification does not exist during the summer months. Temporary stratifications undoubtedly develop from time to time but none was ever detected.

Dissolved oxygen was always found to be adequate at all depths during the summer months (excluding the possibility of its depletion in the zone immediate to the mud-water interface in the deeper portions of the lake). Indications are that it is in plentiful supply at other periods also except during an occasional winter when an abnormally thick and persistent ice-snow cover in conjunction with a low water level may permit oxygen depletion and resultant winterkill of fishes. The water of North Twin Lake is alkaline in reaction, and, depending on various factors, the pH ranges from about 7.6 to 8.4. Ebullition of methane and possibly other gasses is a common occurrence in the areas of deep water at the south end of the lake. Surface temperatures that approached 85°F have been recorded during exceptionally hot summers (e.g., 1955). Bottom temperatures were always found to be within a few degrees of the surface temperatures. The foregoing and other characteristics place North Twin Lake in the Temperate Lake - Order 3 category of Forel's and Whipple's system of lake classification and clearly establish it as eutrophic in accordance with Welch (1952).

METHODS

The plankton organisms from 59 samples collected from 1951 to 1956 (Table 1) were identified. The 1951 to 1954 samples were collected by filtering measured quantities of surface water through a plankton net.

Table 1. Summary of water samples for plankton analysis taken from North Twin Lake, Iowa, during the years 1951-56

Year	Number of samples	Dates collected (Numbers of samples in parentheses)
1951	4*	July 23; August 13; October 6
1952	3*	July 12; 18; 31
1953	1*	September 1
1954	11*	July 7; 19(3); 20; August 2(2); 3; 16(2); 18
1955	37**	June 9; 10; 24(2); July 8; 9; August 2(3); 4; August 15(4); 16; 17; 20(2); 29(2); 30(3); September 12(2); 14(2); 16; 22; 23; October 6(3); 7; 21(3)
1956	3**	March 27; April 15; June 9
Total	59	

*Net samples.

**Centrifuged samples.

The 1955 and 1956 samples were 2-liter samples taken with a Kemmerer sampler at 6 inches below the surface or by submerging a 2.5-liter bottle 6 inches below the surface and allowing it to fill to the 2-liter mark. The plankton in each 2-liter sample was concentrated to about 15 milliliters by means of a Foerst continuous flow centrifuge (1955 model: about 20,000 rpm). The rate of centrifuging was standardized at about one liter per eight minutes. The general procedure was to centrifuge each sample immediately following its removal from the lake and prior to fixation. Very satisfactory fixation was obtained for practically all plankton forms by flooding the concentrate with a very hot 10 per cent formalin solution. Even better results in the fixation of certain zooplankters were obtained later in the study by narcotizing these forms with menthol prior to their fixation with formalin.

The over-all advantages of using the centrifuge method for concentrating plankton samples became quite apparent as the study progressed. The nannoplankton¹ components which probably constitute the bulk of the plankton standing crops of most waters were sampled much more efficiently by this method than they could have been with the usual plankton net.

Most phytoplankton forms occurring in North Twin Lake fall into this category at some time during their life cycle. Many of the Chlorococcales, for example, some *Crucigenia*, most *Oocystis*, *Schroederia*, and *Tetrastrum* are nannoplanktonic at all stages of development. Others such as *Coelastrum* are not necessarily nannoplanktonic when mature but may produce at certain periods large numbers of autocolonies which do fall into this category. Hence net samples containing *Coelastrum* obtained during periods when autospore formation is at a peak would theoretically contain only the largest individuals, resulting in misleading information relative to its abundance. Other important nannoplankton forms not ordinarily captured with the net but easily sampled using the centrifuge method include many diatoms, various protozoans such as minute rhizopods and ciliates, and the minute and abundant colonies of certain blue-green algae.

Several disadvantages are reportedly inherent in the centrifuge method of plankton concentration. It is felt, however, that they are far outweighed by the method's advantages. One purported disadvantage is that the centrifuge is inefficient in concentrating those blue-green algae possessing a very low specific gravity. (Forms containing pseudovacuoles such as *Microcystis* and *Aphanizomenon* fall into this category.) However, frequent checks of centrifuged water consistently indicated little or no loss of any plankton forms. Several double centrifugations also

¹Naumann (1931) designates nannoplankters as those components of the bioeston whose greatest dimension lies between 5 and 60 microns and which can be separated from the water only by sedimentation or centrifugation. Welch (1952) defines nannoplankton as that portion of the plankton which readily passes through number 25 silk bolting cloth (mesh size from .030 to .040 mm). In her study, Ballentine (1953) included small flagellates of less than one micron in length in the nannoplankton. Rodhe (1955) terms these minute and usually overlooked forms the "μ" plankton.

indicated that no residual material remained following initial centrifugings. It might be well to point out, however, that blue-green blooms were not noticeably present in North Twin Lake during the 1955 summer. Perhaps in the presence of excessive amounts of such forms, the centrifuge may lose some of its efficiency in their retention.

Another purported but not necessarily unique disadvantage of the centrifuge method lies in the loss of varying amounts of plankton due to their adhesion to the glassware, etc. used in this method. Errors from such sources are inherent in almost any method. In any event, it is suggested that such errors need not be significant if the proper precautions (such as the use of consistently clean glassware) are taken.

A real disadvantage of the centrifuge method is that all components of the plankton, even finely divided organic and inorganic detritus, are included in the concentrate. The presence of large amounts of detritus often becomes a problem during enumeration since many of the organisms being counted become obscured. By properly diluting the concentrate and occasionally adding a bit of weak detergent solution to break up the concentrate clumps, the presence of large amounts of debris presented no serious problems during the study.

A standard Sedgwick-Rafter counting cell was used in making counts of the plankton organisms and the procedures followed those recommended by the American Public Health Association (1946).

Prior to actual counting, the raw plankton concentrate was diluted to the desired degree and then thoroughly mixed by vigorous agitation. While still agitating the concentrate, a one milliliter portion was withdrawn with a large-bore pipette and introduced into the Sedgwick-Rafter cell. A cover slip which had been lying diagonally across the cell was allowed to move into place during the operation. After permitting the concentrate to settle, enumeration proceeded.

Two magnifications were employed in making the counts, namely, 210X (combination of 10X ocular and 21X (8 mm) objective) and 100X (combination of 10X ocular and 10X (17 mm) objective). The former magnification was successfully used for enumerating all phytoplankton (except occasional large filamentous forms) and protozoans. The latter magnification was used for counting all larger zooplankton such as rotifers and plankton Crustacea. A Whipple ocular micrometer was employed at all times to delimit the "fields" (to be counted) within the Sedgwick-Rafter cell. The microscope used possessed a draw tube which, with the aid of a stage micrometer, permitted calibration of the ocular micrometer so that it covered an area on the bottom of the Sedgwick-Rafter cell of exactly one square millimeter at 100X magnification and an area of exactly 0.25 square millimeter at 210X magnification. In accordance with the findings of Littleford et al. (1940) it was decided that at 210X magnification, counts of organisms in 20 fields selected at "random" from a single one-milliliter concentrate sample would yield fairly reliable estimates of the numbers of each plankton species present in the original lake sample. Counts of the larger zooplankton made at 100X magnification were obtained by examining the entire contents of three successive one-milliliter concentrate samples. The latter technique is called the "survey" method by Welch (1948) and

is used where it is desired to reduce the variability in counts of large, easily identified organisms that are present in small numbers. Factors or multipliers such as described by the American Public Health Association (1946) were computed for each plankton sample analyzed.

An evaluation of the techniques employed in securing numerical and volumetric plankton estimates and measures of their precision is being published in another paper (Kutkuhn, 1958). Plankton volumes were estimated by the "calculated-volume" method described by the American Public Health Association (1946) and Welch (1948).

Throughout the study, every effort was made to identify all forms encountered to species if possible. The use of 210X magnification greatly facilitated identification and counting of even very small forms. It should be pointed out, however, that all plankton forms were carefully identified and studied at higher magnification (if necessary) prior to counting. Occasional doubtful forms encountered during enumeration could often be positively identified while still in the counting cell through judicious use of the 43X (4 mm) objective.

The fact that it is impossible to detect all forms present in fixed samples even at high magnifications was demonstrated when portions of plankton concentrates were stained with a nuclear stain (Delafield's haematoxylin). Numerous small protozoans and motile stages of certain phytoplankton species were found to be present. Obviously, problems arising from an inability to detect many forms are difficult to cope with in studies where complete enumeration of all forms is an objective. Furthermore, as Ballentine (1953) points out, still other forms are completely destroyed when subjected to ordinary fixation. Hence the proper examination of many nanoplankters hinges upon the development of better fixatives and more refined techniques.

The species lists which follow are annotated to give some idea of each species' relative abundance during the study period. Adjectives such as common and uncommon are used to indicate the frequency with which the various forms appeared in the samples and may or may not be validly descriptive of how these forms were actually distributed throughout the lake. In addition, the lists are supplemented by the inclusion of forms encountered only when analyzing fish digestive tract contents. Certain of these forms are not truly planktonic and may only on rare occasions be tychoplanktonic. They are included mainly to add to the completeness of the floral and faunal listings.

The gizzard shad, *Dorosoma cepedianum*, was very abundant in North Twin Lake in 1954 and 1955 and these plankton studies were made, to a considerable extent, in an attempt to determine the ecological relationships of this fish. All plankton species encountered during shad digestive tract analyses are denoted with an asterisk (*). It will be noted as the lists are reviewed that shad include a remarkably large number of plankton forms in their diet. Such a characteristic has led Tiffany (1921, p. 115) to remark that "... the gizzard shad is about the most wonderful tow net that one could desire to get an estimate of the kinds and proportionate numbers of microscopic algae present in a body of water."

The 1955 numerical estimates for each species are summarized in the annotated list. These counts represent the numbers of individual organisms per milliliter of water.

Although most samples were taken from the littoral areas of the lake, it is believed that the species lists are reasonably complete as regards the plankton populations of the entire lake. Those samples obtained from limnetic situations usually contained, for the most part, the same forms encountered in the littoral samples.

The Phytoplankton

All phytoplankton forms were identified by the author. However, special thanks are due Dr. J. D. Dodd, Department of Botany, Iowa State College and Dr. G. W. Prescott, Department of Botany and Plant Pathology, Michigan State University, for confirming determinations of certain algae.

The classification of the phytoplankton exclusive of the Bacillariophyceae (diatoms) and Desmidiaceae (desmids) is that given by Prescott (1951). Practically all genera and most species and varieties of the Cyanophyta, Chlorophyta, and Mastigophora (Phytomastigophorea) were identified using Prescott's (1951) keys and descriptions. Other important works were referred to where necessary. Thus certain species of the Cyanophyta were identified using the keys and descriptions of Geitler (1925, 1932) and Huber-Pestalozzi (1938). The latter work was also used to identify several planktonic fungi. With one exception all species of Euglena were determined through the use of keys and descriptions given by Johnson (1944).

To aid in identifying certain diatoms, the sulphuric acid-bichromate method described by Hohn (1951) for cleaning diatom frustules proved to be very useful. Most diatom genera were determined with the aid of keys formulated by the same author. Several genera and all diatom species and varieties were identified using the excellent works of Husted (1930) and Huber-Pestalozzi (1942).

Determinations of all genera and most species and varieties of the Desmidiaceae were made with the aid of keys and descriptions given by Smith (1924).

In addition to the foregoing, the general works of Smith (1950) and Tiffany and Britton (1952) were of value as supplementary references.

Division CYANOPHYTA

Myxophyceae

Chroococcales:

*Aphanocapsa delicatissima West and West—Very common, especially in midsummer when it may constitute the bulk of the phytoplankton (as, e.g., in 1955). 27-80 (June and July); 4, 325-19, 900 (August to October 6); 306-600 (October 21).

*Aphanocapsa pulchra (Kütz.) Rabenhorst—Common but not nearly as common as A. delicatissima. 0-72 (June-September).

*Aphanocapsa rivularis (Carm.) Rabenhorst—In sample taken in July, 1952. One occurrence in shad digestive tract (1955).

*Aphanothece gelatinosa (Henn.) Lemmermann—One colony found in shad digestive tract (1955).

- *Aphanothece nidulans P. Richter—Infrequent occurrences during summer and fall months, occasional in spring. 0-5 (July 9, August 2, September 16).
- *Aphanothece saxicola Naegeli—One colony found in shad digestive tract (1955).
- *Chroococcus limneticus Lemmermann—Common during summer and fall months. 0-16 (June-July); 15-120 (August); 0-27 (September-October).
- Coelosphaerium dubium Grunow—Specimens found in samples taken in July, 1952 and June, 1955. 2 (June 24).
- *Coelosphaerium kuetzingianum Naegeli—Uncommon. 0-10 (June-October).
- *Coelosphaerium naegelianum Unger—Common in summer, especially in 1951 and 1952. 0-9 (June-September).
- Dactylococcopsis fascicularis Lemmermann—Individual cells are quite difficult to distinguish from certain species of Ankistrodesmus (Chlorophyta). Seemingly common in spring.
- Dactylococcopsis rhophidioides Hansgrig—Apparently quite common in early spring.
- Gomphosphaeria lacustris Chodat—Frequent, especially during late spring and early summer. 0-46 (June 24-August 15); 10-84 (August 16-September 22); 0-6 (September 23-October 21).
- Marssoniella elegans Lemmermann—In sample taken in August, 1955. 10 (August 16).
- *Merismopedia glauca (Ehrenb.) Naegeli—Common. 5 (September 14).
- *Merismopedia tenuissima Lemmermann—Very common during much of the year. 0-15 (June-July); 108-792 (August 2-20); 438-2123 (August 29-September 16); 120-570 (September 22-October 21).
- *Microcystis aeruginosa Kütz.—Very common, especially during the summers of 1951, 1952, and 1953. 0-27 (June-October).
- *Microcystis incerta Lemmermann—In sample taken in July, 1952. Rare in shad digestive tracts (1955).
- *Synechococcus aeruginosus Naegeli—In sample taken in June 1955.

Hormogonales:

- *Anabaena circinalis Rabenhorst—Infrequent in plankton samples, common in shad stomachs - June, 1955.
- *Anabaena spiroides var. crassa Lemmermann—Very common during early summer. 605 (July 8) otherwise 0-30 (June 24-August 2).
- *Anabaena sp.—A form having straight trichomes, very infrequent (1955). (Only specimens with sterile trichomes were found.) 2 (June 9).
- *Anabaenopsis circularis (G.S.W.) Wol. and Miller—Fairly common in mid- and late summer (1955). 18-213 (August 15-October 6); 3-9 (October 21) (These counts also include A. elenkini).
- *Anabaenopsis elenkini V. Miller—Fairly common, occurring mostly in late summer (1955).
- *Aphanizomenon flos-aquae (L.) Ralfs—Common during summer months. 40-160 (June 24-July 9); 0-27 (August 2-October 6).

- *Lyngbya aerugineo-caerulea (Kütz.) Gomont-Tychoplankter, no occurrences in plankton samples. In shad digestive tract (1955).
- *Lyngbya contorta Lemmermann-Very common during summer months (1955). 1 (June 9); 0 (June 10-August 4); 0-24 (August 15-29); 210-1290 (August 29-October 6); 45-52 (October 21).
- Nostoc sp. -Rare in plankton. Occurred twice in samples taken in September, 1955. 0-9 (September 12-16).
- *Oscillatoria limnetica Lemmermann-Very common during summer months. 18-360 (August 29-October 21).
- Oscillatoria limosa (Roth) C. A. Agardh-One filament in sample taken in April, 1956.
- *Oscillatoria prolifica (Grev.) Gomont-Common in shad digestive tracts (June, 1955).
- Oscillatoria sp. -In samples taken in April, 1956.
- *Phormidium mucicola Naumann and Huber-Pestalozzi-Common in mucilage of Microcystis aeruginosa.
- Spirulina nordstedtii Gomont-A single occurrence in September, 1955.
- *Spirulina princeps (West and West) G. S. West-One occurrence in August, 1955.

Fungi

- (?) Asterothrix raphidioides (Reinsch) Printz-Common in early spring (1956).
- *Planctomyces sp. -Very infrequent occurrences in samples taken during the 1955 summer and fall.
- *Fungus spores (Unidentified)-Common in the 1955 samples.

Division CHLOROPHYTA

Chlorophyceae

Tetrasporales:

- *Gloeocystis gigas (Kütz.) Lagerheim-Common in spring and early summer. 0-28 (June); 0 (July); 13-90 (August 2-20); 0-25 (August 29-October 21) (These counts also include G. major.)
- *Gloeocystis major Gerneck ex Lemmermann-Common in spring and early summer.
- *Gloeocystis vesiculosa Naegali-One colony collected in October, 1955.
- Sphaerocystis schroeteri Chodat-Fairly common in spring and early summer. 4-15 (June); 2 (August 2); 6 (August 15).

Ulotrichales:

- *Ulothrix aequalis Kützing-Tychoplankter. Found in shad digestive tracts, (1955).

Chaetophorales:

- *Stigeoclonium subsecundum Kützing-Tychoplanktonic. Found only in shad digestive tracts (1955).

Cladophorales:

- *Cladophora insignis (C. A. Ag.) Kützing-Tycho plankter. Not encountered in plankton samples. Occurred in shad digestive tract (1955).
- *Pithophora oedogonia (Mont.) Wittrock-In shad digestive tract (1955).

Oedogoniales:

- *Oedogonium sp. - Found only in shad digestive tracts (1955).

Chlorococcales:

- Actinastrum hantzschii Lagerheim-One occurrence in April, 1956.
- *Ankistrodesmus falcatus (Corda) Ralfs-Very common during spring, early summer, and fall. 35-240 (June 9-August 4); 0-60 (August 15-October 6); 1683-2019 (October 21) (These counts also include the following two forms).
- *Ankistrodesmus falcatus var. mirabilis (West and West)-Common in spring and early summer.
- *Ankistrodesmus falcatus var. stipitatus (Chod.) Lemmermann-Fairly common in spring and early summer.
- Botryococcus sudesticus Lemmermann-Rare. 5 (August 16); 5 (September 14).
- Characium ambiguum Hermann-Epiphytic on Melosira filaments but often found free in plankton concentrates.
- Characium gracilipes Lambert-Tycho planktonic. Very common in spring.
- *Coelastrum cambricum Archer-Very common at all periods. 0-18 (June-October).
- *Coelastrum microporum Naegeli in A. Braun-Very common at all periods. 2-12 (June-July); 10-113 (August-September 14); 0-12 (September 16-October 21).
- *Coelastrum reticulatum (Dang.) Senn-Relatively uncommon in plankton samples (1955). 5 (August 17).
- *Crucigenia crucifera (Wolle) Collins-Common during summer months. 6-8 (August 15); 5-36 (August 20-September 23).
- *Crucigenia irregularis Wille-Rare. One or two occurrences in 1955.
- *Crucigenia quadrata Morren-Very common - the most frequently occurring species of Crucigenia. 0-60 (June-October).
- *Dictyosphaerium ehrenbergianum Naegeli-Frequent to common in spring and summer. 0-65 (June 24-October 21) (These counts also include D. pulchellum).
- *Dictyosphaerium pulchellum Wood-Common in spring and summer.
- *Dimorphococcus lunatus A. Braun-Fairly common in early summer. 1 (June 24).
- *Franceia droescheri (Lemm.) G. M. Smith-Frequent occurrences in spring and summer (1955). 0-8 (August 2-20).
- *Golenkinia paucispina West and West-Fairly common, occurring with G. radiata. 15-126 (August 2-30); 195-525 (September-October) (These counts also include G. radiata).

- *Golenkinia radiata (Chod.) Wille—Common, especially in spring and fall.
- *Kirchneriella contorta (Schmidle) Bohlin—Very infrequent in occurrence.
- *Kirchneriella lunaris (Kirch.) Möbius—Common throughout the summer and fall months. 0-12 (July 8-August 30); 25-125 (September 12-16); 0-15 (September 22-October 21).
- *Kirchneriella obesa (W. West) Schmidle—Fairly common during the summer months. 0-54 (August 2-October 21) (These counts may also include other Kirchneriella spp.).
- Kirchneriella subsolitaria G.S. West—Infrequent occurrences during the summer months.
- *Lagerheimia ciliata (Lag.) Chodat—Fairly common during spring, summer, and fall months. 0-25 (August 2-August 30) (These counts include other Lagerheimia spp.)
- *Lagerheimia citrififormis (Snow) G.M. Smith—Frequent occurrences in plankton samples and in shad digestive tracts.
- *Lagerheimia longiseta (Lemm.) Printz—Occurring with L. ciliata.
- *Lagerheimia quadriseta (Lemm.) G.M. Smith—Common. Occurring with L. ciliata.
- Micractinium pusillum Fresenius—Fairly common in late spring and early summer. 2-10 (June-July); 0-16 (August 2).
- *Nephrocystium agardhianum Naegeli—Frequent occurrences during late summer. 15 (September 22); 6 (October 6).
- *Oocystis borgei Snow—Very common in early summer (1955).
- *Oocystis lacustris Chodat—Infrequent occurrences in summer and fall (1955).
- *Oocystis parva West and West—Very common in spring and early summer - the most common species of Oocystis. 214-519 (June); 8-102 (July-August 4); 245-354 (August 15-20); 10-63 (August 29-October 21). (These counts include other Oocystis.)
- *Oocystis submarina Lagerheim—Very common in early summer.
- *Pediastrum biradiatum Meyen—Not encountered in plankton samples but found in shad digestive tracts (1955).
- *Pediastrum boryanum (Turp.) Meneghini—Fairly common in all samples. 0-50 (June-September 22).
- *Pediastrum duplex Meyen—Very common in all samples. 3-90 (June-October 21) (These counts include the two following forms).
- *Pediastrum duplex var. clathratum (A. Braun) Lagerheim—This and the following variety of P. duplex were the most frequently occurring forms of Pediastrum in the North Twin Lake collections.
- *Pediastrum duplex var. gracilimum West and West—Occurring with P. d. clathratum.
- *Pediastrum simplex (Meyen) Lemmermann—Frequent occurrences in all samples. 0-24 (June 10-October 6) (These counts include the following form).
- *Pediastrum simplex var. duodenarium (Bailey) Rabenhorst—Common in most samples.
- *Planktosphaeria gelatinosa G.M. Smith—Infrequent to common during spring and summer. 2-5 (June 24-July 8); 5 (August 16).

- Quadrigula closteroides (Bohlin) Printz—Apparently rare. Occurred in sample taken in September, 1953.
- Quadrigula lacustris (Chod.) G. M. Smith—Sporadically common in spring (1956).
- *Scenedesmus abundans (Kirch.) Chodat—Very common. Occurred in all plankton samples. 1-16 (June); 28-729 (July-October 21) (These counts also include S. quadricauda).
- *Scenedesmus abundans var. asymmetrica (Schroed.) G. M. Smith—In shad digestive tract (1955).
- *Scenedesmus abundans var. longicauda G. M. Smith—Very common. In most samples.
- *Scenedesmus acuminatus (Lag.) Chodat—Fairly common in mid-summer, 1955. 0-5 (June-July); 54-468 (August 2-October 21) (These counts also include S. dimorphus).
- Scenedesmus arcuatus Lemmermann—Frequent occurrences in 1955 samples.
- *Scenedesmus bijuga var. alternans (Reinsch) Hansgirg—Very common during spring, summer, and fall months. 0-4 (June); 5-70 (July-August 17); 0-30 (August 20-October 6); 57-66 (October 21).
- *Scenedesmus bijuga var. flexuosus (Lemm.) Collins—Fairly common in early spring, 1955. 3-8 (June-July 8); 6 (August 20).
- *Scenedesmus denticulatus Lagerheim—Common in spring and summer. 0-10 (June-September 22); 102-108 (October 21).
- *Scenedesmus denticulatus var. ? —This form is apparently a new variety (or species?) and is being currently studied by Dr. G. W. Prescott.
- *Scenedesmus dimorphus (Turp.) Kütz.—Very common, occurring in all samples.
- *Scenedesmus quadricauda (Turp.) Bréb.—Very common, occurring in all samples.
- *Scenedesmus quadricauda var. maximus West and West—Occasional occurrences in plankton samples and in shad digestive tracts (1955).
- *Schroederia setigera (Schroed.) Lemmermann—Common to very common throughout the spring and summer, 1955. 44-110 (June-July); 2-32 (August 2-17); 0-27 (August 20-October 21).
- *Selanastrum gracile Reinsch—Common during summer months. 0-45 (August 2-30).
- Selanastrum westii G. M. Smith—Seemingly quite rare. One or two occurrences in samples taken in 1955.
- *Sorastrum spinulosum Naegeli—Rare in plankton samples and in shad digestive tracts (1955).
- Tetradesmus smithii Prescott—Frequent occurrences in early summer samples (1955). 20 (August 2); 6 (August 20).
- *Tetraëdron caudatum var. longispinum Lemmermann—Very common. 0-15 (July 8-September 23); 48-63 (October 21).
- Tetraëdron enorme (Ralfs) Hansgirg—Infrequent occurrences in 1955 samples. 12 (August 29).
- Tetraëdron gracile (Reinsch) Hansgirg—Uncommon.
- *Tetraëdron hastatum (Reinsch) Hansgirg—Common. 0-36 (August 15-October 21).

- *Tetraëdron hastatum var. palatinum (Schmidle) Lemmermann-common.
- *Tetraëdron limneticum Borge-Common during summer months. 0-26 (June 9-August 17).
- *Tetraëdron minimum (A. Bruan) Hansgirg-Uncommon.
- *Tetraëdron muticum var. punctulatum (Reinsch) De Toni-Found in shad digestive tracts, 1955.
- *Tetraëdron planctonicum G.M. Smith-Infrequent occurrences in 1955 samples.
- *Tetraëdron regulare Kütz.-Very common. The most frequently occurring species of Tetraëdron. 2 (June 10); 8-36 (July 8-September 12); 0-6 September 14-October 21).
- *Tetraëdron trigonum (Naeg.) Hansgirg-Uncommon.
- *Tetrastrum staurogeniaeforme (Schroeder) Lemmermann-Fairly common in spring and fall (1955). 5 (August 4); 5 (August 29); 0-87 (September 12-October 21).

Zygnematales:

Zygnemataceae:

- *Mougeotia sp.-Tycho planktonic. Frequent in samples taken in fall (1955). 0-1 (September 22-October 21).
- *Spirogyra sp.-Tycho planktonic. Very infrequent in plankton samples, occasionally common in shad digestive tracts (1955). (October 21).

Desmidiaceae:

- *Closterium acerosum (Schrank) Ehrenb.-Common in digestive tracts of shad collected in June, 1955.
- Closterium gracile var. elongatum W. and G.S. West-Common in plankton sample taken in June, 1956.
- *Closterium moniliferum (Bory) Ehrenb.-Common in early summer (1955).
- *Closterium spp.-Includes several forms of very rare occurrence (1955).
- *Cosmarium cyclicum var. nordstedtianum (Reinsch) W. and G.S. West-Uncommon. 0-5 (June 9-September 12).
- *Cosmarium punctulatum var. subpunctulatum (Nords.) Börg.-In shad digestive tracts (1955).
- *Cosmarium reniforme (Ralfs) Archer-Fairly common in early summer (1955).
- *Staurastrum paradoxum Meyen-Common during the spring, summer, and fall months. (The most common species of Staurastrum).
- *Staurastrum spp.-Several forms of rare occurrence in 1955 samples none of which were isolated for identification to species. 3-10 (June 9-August 2); 10-52 (August 4-20); 0-18 (August 29-October 21).

Division CHRYSOPHYTA

Xanthophyceae

Ophiocytium capitatum var. longispinum (Möbius) Lemmermann—
One specimen encountered in 1955 samples. 10 (August 29).

Bacillariophyceae

Centrales:

- *Cyclotella comta (Ehrenb.) Kütz. —Fairly common in spring and fall. 0-24 (June 9-August 29); 5-96 (August 30-October 21) (Counts include C. meneghiniana).
- *Cyclotella meneghiniana Kütz. —Common in spring and fall.
- *Melosira ambigua (Grun.) O. Müller—Common in spring and fall.
- *Melosira granulata (Ehrenb.) Ralfs—The most common species of Melosira; common to abundant in spring and fall. 36-642 (June 9-October 21) (Counts include M. ambigua).
- *Melosira granulata var. angustissima Müller—Very common during the 1952 summer.
- Rhizosolenia eriensis H. L. Smith—Seemingly very common in early spring (1956).
- *Stephanodiscus astraea (Ehrenb.) Grun. —Very common in spring and fall. 91-860 (June); 12-132 (July-September 12); 0-18 (September 14-October 21) (Counts include S. niagarae).
- *Stephanodiscus niagarae Ehrenb. —Very common to extremely abundant in spring. Fairly common in fall.

Pennales:

- *Achnanthes spp. —Includes several minute forms of very infrequent occurrence (1955).
- Amphipleura pellucida Kütz. —Uncommon. Infrequent occurrences in 1955 samples. 0-9 (June 24-August 30).
- *Amphiprora ornata Bailey—Common in spring, early summer, and fall. 2-5 (June); 0-8 (August 2-October 6).
- *Amphora ovalis Kütz. —Fairly common in spring (1955, 1956). 0-8 (June 9-August 4); 0-3 (October 21).
- *Asterionella formosa Hassall—Very common during mid-spring. 2 (June 9).
- *Bacillaria paradoxa Gmel. —In samples taken in September, 1953 and April, 1956.
- *Caloneis silicula (Ehrenb.) Cleve—Found in shad digestive tracts (1955).
- *Cymatopleura elliptica (Bréb.) W. Smith—Frequent to common in spring and fall. 0-9 (June 9-September 16).
- *Cymatopleura elliptica fo. spiralis (Chase) Boyer—Occasional occurrences in samples taken during the summers of 1954 and 1955.
- *Cymatopleura solea (Bréb.) W. Smith—Common in spring and fall. 12 (October 6).

- *Cymbella ehrenbergii Kütz. -Probably the most common species of Cymbella, especially in the spring. 2-35 (June 9-August 16); 0-24 (August 17-October 21) (Counts include other Cymbella spp.).
- *Cymbella tumida (Bréb.) Van Heurck -Fairly common in early spring (1956).
- *Cymbella turgidula Grun. -One of the more common species of Cymbella (1955).
- *Cymbella spp. -Includes several forms of seemingly common occurrence in 1955 samples.
- *Epithemia argus Kütz. -Uncommon (1954, 1955).
- *Epithemia zebra (Ehrenb.) Kütz. -Common during spring, summer, and fall. 0-5 (June 10-October 21).
- *Eunotia lunaris (Ehrenb.) Grun. -In shad digestive tracts only.
- *Eunotia pectinalis var. minor (Kütz.) Rabenhorts -In shad digestive tracts.
- *Eunotia sp. -Frequent occurrences in 1954 and 1955 samples.
- Fragilaria capucina Desmaz. -Encountered only in spring and early summer plankton samples.
- Fragilaria construens (Ehrenb.) Grun. -Found in shad digestive tract (1955).
- *Fragilaria crotonensis Kitten -Very common in early summer. (The most common of the Fragilaria species). 2-27 (June-July); 0-18 (August 16-October 6).
- Fragilaria virescens Ralfs -Occasional occurrence in early spring samples (1956).
- *Gomphonema sp. -Uncommon in the plankton. 6 (August 20); 6 (October 6).
- *Gyrosigma attentuatum (Kütz.) Cleve -Very common in early spring, common throughout summer months. 2-5 (June-July); 5 (August 17).
- *Navicula bicapitellata Hust. -Common throughout the 1955 summer.
- *Navicula cryptocephala Kütz. -Common in early spring (1956).
- *Navicula cuspidata Kütz. -Very common in early spring (1956). 6 (August 20); 10 (August 29); 45 (September 12).
- *Navicula rheinhardtii Grun. -Seemingly quite common during the 1955 summer. 2-73 (June-July); 45-332 (August 2-16); 0-110 (August 17-October 21) (Counts include other Navicula spp.).
- *Navicula spp. -Includes several more or less rare forms which were not identified to species.
- *Neidium dubium (Ehrenb.) Cleve -In shad digestive tracts (October, 1955).
- *Neidium iridis var. ampliata (Ehrenb.) Cleve -Very infrequent in samples taken during the 1955 summer.
- *Nitzschia acicularis W. Smith -Relatively common. (Sometimes difficult to distinguish from Synedra acus under low power.)
- *Nitzschia sigma (Kütz.) W. Smith -Fairly common in spring and fall (1954, 1955). 2 (June 9); 5 (August 16); 5-10 (September 16-22).
- *Nitzschia sigmoidea (Ehrenb.) W. Smith -Common, especially in fall. 1 (June 10); 3 (July 9); 6 (August 30).
- *Nitzschia spp. -Includes one or two forms of infrequent occurrence. 1-15 (June-July); 0-36 (August 17-30); 5-25 (September 14-October 21).

- *Pinnularia major Kütz. -Common in spring and fall.
- *Pinnularia spp. -Includes several occasionally common forms which could not be identified to species because of time limitations. 0-36 (June 9-October 6).
- *Rhopalodia gibba (Ehrenb.) O. Mull. -In samples taken in early spring (1956).
- *Stauroneis acuta W. Smith -In shad digestive tract (1955).
- *Surirella biseriata Bréb. -Common to abundant, especially during spring months. 0-3 (June); 3 (August 2); 6 (October 21).
- *Surirella biseriata var. bifrons (Ehrenb.) Hust. -Fairly common in early spring.
- *Surirella linearis W. Smith -Common in early spring and fall. 24-36 (October 6-21).
- *Surirella tenera Greg. -Common in spring and early summer. 2-8 (June-July); 3 (August 15).
- *Surirella spp. -Includes several less common forms of sporadic abundance. 1 (June 24); 9 (August 30).
- *Synedra acus Kütz. -Very common throughout most of the spring, summer, and fall.
- *Synedra oxyrhynchus Kütz. -Seemingly very common at all periods.
- *Synedra ulna (Nitzsch.) Ehrenb. -Very common to abundant in most plankton samples.

PROTOZOA

Mastigophora

Phytomastigophorea

Chrysomonadida:¹

Dinobryon sertularia Ehrenb. -One occurrence in spring of 1955.
1 (June 24).

*Mallomonas pseudocoronata Prescott -Frequent in samples taken in early spring and late fall. 5 (September 14); 3 (October 21).

Dinoflagellida:²

Ceratium hirundinella (O. F. M.) Dujardin -Common during summer months.

Glenodinium armatum Levander -Fairly common in early spring (1956).

Glenodinium gymnodinium Penard -Frequent in spring and early summer samples. 0-10 (June 24-August 4).

*Glenodinium kulczynskii (Wolosz.) Schiller -Occasional occurrences in summer samples. 6 (August 30); 5 (September 22).

*Glenodinium pulvisculus (Ehrenb.) Stein. -Very common in spring and fall. 0-40 (August 15-October 21).

¹Corresponds to algal Class Chrysophyceae, Division Chrysophyta.

²Corresponds to algal Class Dinophyceae, Division Pyrrophyta.

*Glenodinium quadridens (Stein) Schiller—Very common to abundant in early and mid-summer. (This was the most common species of Glenodinium). 2-5 (July); 10-175 (August); 9-10 (September 12-14).

Phytomonadida:¹

Carteria klebsii (Dang.) Dill—Occasional occurrences in mid-spring samples.

Chlamydomonas globosa Snow—Very common in early spring (1956).

Chlamydomonas snowii Printz—Frequent in early spring samples (1956).

Chlamydomonas spp.—Includes one or two species that are relatively common in spring and fall.

Coccomonas orbicularis Stein—Infrequent occurrences in early summer samples. 0-160 (August 2-29).

*Eudorina elegans Ehrenb.—Very common sporadically in spring and early summer. 3 (June 9); 3 (August 2).

Pandorina morum (Müll.) Bory—Very common sporadically as indicated, for example, by a sample taken in mid-July, 1952.

*Phacotus lenticularis (Ehrenb.) Stein—Very common in spring and early summer. 5 (September 22).

Euglenida:²

Astasia sp.—Common in early spring (1956).

Anisonema emarginatum Stokes—Common in early spring (1956).

*Euglena acus Ehrenb.—Fairly common in late summer (1955).

*Euglena cysts—0-16 (July 8-August 29).

*Euglena ehrenbergii Klebs—Very common during spring and summer months. 0-6 (June 24-October 21).

*Euglena gracilis Klebs—Very common during spring and summer months. 0-168 (July 8-October 21).

*Euglena intermedia Klebs—Common in fall (1955). 0-5 (September 14-October 21).

Euglena minuta Prescott—Fairly common in spring and fall.

*Euglena oxyuris Schmarida—Common to abundant during summer months (1955). 0-4 (June 9-October 21) (Counts include E. tripteris).

*Euglena tripteris Dujardin—Very common during summer months (1955).

*Lepocinclis acuta Prescott—Occasional occurrences in samples taken in the fall of 1955 and spring of 1956.

*Lepocinclis ovum (Ehrenb.) Lemmermann—Very common in spring and early summer. 0-60 (June 9-October 21).

*Phacus acuminatus Stokes—Common during summer months. 12-81 (August 15-30); 0-18 (September 12-October 21) (Counts include P. curvicauda).

¹Corresponds to algal Class Chlorophyceae (Order Volvocales), Division Chlorophyta.

²Corresponds to algal Division Euglenophyta.

- *Phacus acuminatus var. drezipolskii Skvortzow—Common in summer plankton samples and in shad digestive tracts.
- *Phacus chloroplastes Prescott—Infrequent in early spring samples, fairly common in fall. 5 (September 22).
- *Phacus curvicauda Swirenko—Fairly common during 1955 summer.
- *Phacus helicoides Pochmann—A single specimen found in shad gizzard.
- *Phacus longicauda (Ehrenb.) Dujardin—Fairly common in early summer. 0-25 (June 24-August 20).
- *Phacus orbicularis Huebner—Very infrequent in 1955 samples.
- Phacus pseudoswirenkoi Prescott—Occasional occurrences in early spring samples (1956).
- *Phacus pyrum (Ehrenb.) Stein—Common in early spring (1956). 27 (August 30); 5 (September 23); 9 (October 21).
- *Phacus swirenkoi Skvortzow—Common in plankton samples and shad digestive tracts (1955).
- *Phacus spp. 1 (June 10); 0-72 (August 2-September 23) (In some counts species were not all identified).
- *Phacus tortus (Lemm.) Svortzow—Very infrequent occurrences in 1955 samples.
- Scytomonas pusilla Stein—Common in early spring (1956).
- *Trachelomonas granulosa Playfair—Fairly common during summer months.
- *Trachelomonas volvocina Ehrenb.—Common during spring, summer, and fall months.
- *Trachelomonas spp.—Includes several common but unidentified species. 0-8 (June 9-August 2); 5 (September 22); 3 (October 21) (Counts include above two species).

Zoomastigophorea

Rhizomastigida:

- *Multicilia lacustris Lauterborn—Apparently rare. In one or two samples taken in the spring of 1955.

The Quotient Hypothesis as an aid in establishing the trophic status of North Twin Lake

In recent years, much attention has been given the prospect of designating the trophic nature of lakes on the basis of phytoplankton species composition. A large amount of limnological research has prompted the conclusion that each of the several phytoplankton taxa attains its best development species-wise under varying combinations of environmental conditions. It is well known for example that the Cyanophyta, the Chlorococcales of the Chlorophyta, the Euglenida, and the Centrales of the Bacillariophyceae possess what is known as a eutrophic tendency. On the other hand, the Desmidiaceae of the Chlorophyta and the Pennales of the Bacillariophyceae generally exhibit strong oligotrophic tendencies. On the basis of such information, quotients involving the numbers of species of certain phytoplankton taxa have been formulated so as to reflect the trophic nature of aquatic environments (e. g. Thunmark, 1945; Nygaard, 1949).

Since many of the assumptions relative to the trophic tendencies of certain of the phytoplankters involved in these quotients have been found to be invalid due to the wide ranges of conditions under which some of these organisms (eurybionts) can exist, the method has been subjected to some criticism (Rawson, 1956b). Nygaard (1955) himself questioned the validity of the method when he determined that his "compound quotient" failed to exhibit good agreement in the middle of the trophic range when compared with results of another method (photosynthetic activity) for ascertaining trophic types. The quotient methods have by no means been discarded, however, and it is believed that for most situations such criteria have a definite usefulness. They should continue to be improved upon as more information regarding trophic preferences of phytoplankton is acquired.

Since a considerable amount of information concerning the species composition of the North Twin Lake phytoplankton has been obtained, it was felt that the application of one of the aforementioned phytoplankton quotients might be helpful in ascertaining more precisely the trophic nature of the lake. Of the several quotients that have been devised, the compound quotient proposed by Nygaard (1949) was selected as probably being the most accurate for this purpose. The formula for this quotient is:

Compound Quotient =

$$\frac{\text{Myxophyceae} + \text{Chlorococcales} + \text{Centrales} + \text{Euglenida} + \text{Desmidiaceae}}{11}$$

where each taxon is represented by the number of species it comprises in the particular body of water being studied. Applying the quotient to the North Twin Lake data we obtain:

$$\text{Compound Quotient} = \frac{35 + 72 + 8 + 26}{11} = \frac{141}{11} = 12.8$$

which indicates, according to Nygaard, that North Twin Lake is distinctly eutrophicated and may even be somewhat contaminated.

It is emphasized by Nygaard that this quotient should not ordinarily be used alone but should be regarded as supplementary to other limnological data. Hence the quotient obtained above helps to definitely substantiate the lake's trophic status which was previously determined on the basis of more general characteristics.

The estimated volumes (Table 2) indicate that diatoms constituted the bulk of the plankton (32.5 per cent). However, the diatoms were abundant only in the spring when *Stephanodiscus niagarae* and *Melosira granulata* comprised a major part of the plankton. Blue-green algae were second in total plankton bulk (30.9 per cent) and their peak was in midsummer. *Aphanocapsa delicatissima* (Fig. 1) was by far the most important species in 1955. This form attained its best development toward the end of August. Although it was very abundant during this period, this blue-green alga never developed into bloom proportions.

Table 2. Summary of North Twin Lake plankton, 1955—composition by major taxa

Taxon	No. of species*	Per cent of total volume		
		Phytoplankton	Zooplankton	Plankton
Phytoplankton	236	100.0	-	84.3
Cyanophyta	35	36.6	-	30.9
Chlorophyta	93	18.6	-	15.7
Chrysophyta	62	38.6	-	32.5
Fungi	3	trace	-	trace
Mastigophora	43	6.2	-	5.2
Zooplankton	122	-	100.0	15.7
Protozoa	44	-	27.9	4.4
Rotatoria	49	-	54.9	8.6
Crustacea	20	-	16.4	2.6
Other	9	-	0.8	0.1
Total plankton	358	-	-	100.0
Tripton	-	-	-	308.2

Ratio of phytoplankton volume to zooplankton volume: 5.4:1.

*Includes all species encountered during the period 1951-1956.

Other blue-greens that contributed measurably to the phytoplankton but only for relatively short periods included *Anabaena spiroides*, *Anabaenopsis elenkini*, and *Aphanizomenon flos-aquae*. *Microcystis aeruginosa*, usually a trouble-maker in North Twin Lake, was noticeably reduced in abundance in 1955. The highest volume for this form was recorded on June 24.

It might be pointed out here that even though the blue-green algae comprised a major portion of the North Twin Lake plankton during the 1955 summer, objectionable forms such as *Microcystis*, *Anabaena*, *Aphanizomenon*, and *Coelosphaerium* were either consistently reduced or were abundant only for very short periods, never attaining bloom proportions. These high-floating conspicuous forms were replaced in the plankton by other less conspicuous and less bouyant forms such as the dominant *Aphanocapsa delicatissima*.

Green algae (*Chlorophyta*) were represented during the 1955 summer by a greater number of species than that possessed by any other taxon but constituted a relatively small portion of the bulk of the phytoplankton and total plankton volumes. Important components of the green algae from the volumetric standpoint were species of *Oocystis* (Fig. 1), *Pediastrum*, *Scenedesmus*, *Coelastrum* (Fig. 1), and *Golenkinia*. Highest development of green algae seemed to occur during October.

Flagellates contributed little to total plankton (5.2 per cent) volumes but were well represented in most samples. Volumetrically, the most important of these forms were Euglena spp., especially E. tripteris (Fig. 1) and E. gracilis (Fig. 1), Phacus spp., and Glenodinium quadridens (Fig. 1).

The Zooplankton

All zooplankton identifications were made by the author with the assistance of Dr. E. R. Becker, Iowa State College, who confirmed determinations of certain protozoan genera; Dr. W. T. Edmondson, University of Washington, who verified the identification of the rotatorian species, Anuraeopsis fissa Gosse; and Dr. M. J. Ulmer, Iowa State College, who assisted in identifying distorted specimens of the rotatorian species, Asplanchna priodonta Gosse.

The classification of the amoeboid and ciliate Protozoa is that followed by Hall (1953). Generic determinations of these forms were based upon the keys of Pennak (1953) and the keys and descriptions of Kudo (1954). Certain Sarcodina species were determined with the aid of keys given by Edmondson (1918). The very fine work of Kahl (1930-35) was helpful in identifying several species of the Ciliophora.

Rotatorian genera were determined with keys formulated by Pennak (1953). Specific determinations of Rotatoria necessitated the use of keys and/or descriptions given by many authors and widely scattered throughout the literature. The various works referred to in the present study and the genera they covered were: Ahlstrom (1940), Brachionus; Ahlstrom (1943), Keratella; Beauchamp (1932), Ascomorpha; Carlin (1939), Colurella; Carlin (1943), Polyarthra; Harring (1916), Lepadella; Harring and Myers (1926), Lecane and Monostyla; Hudson and Gosse (1886), Macrochaetus and Philodina; and Rylov (1935), all others.¹

Cladocera, Copepoda, and miscellaneous invertebrates other than Crustacea were identified with keys given by Pennak (1953). The keys and descriptions of Hoff (1942) were used to identify the few Ostracoda encountered.

1

Just prior to presstime, the following important work appeared which is destined to be a boon to all planktologists, limnologists, invertebrate zoologists, and biologists in general; "Rotatoria. Die Rädertiere Mitteleuropas" by M. Voigt. 1956-57. Gebrüder Borntraeger, Berlin-Nikolassee. I Textband mit 27 Textabbildungen, 508 S. u. II Tafelband mit 115 Tafeln. This treatise consolidates most if not all major works on Rotatoria and includes keys to and descriptions of practically all known species of this highly cosmopolitan group of animals.

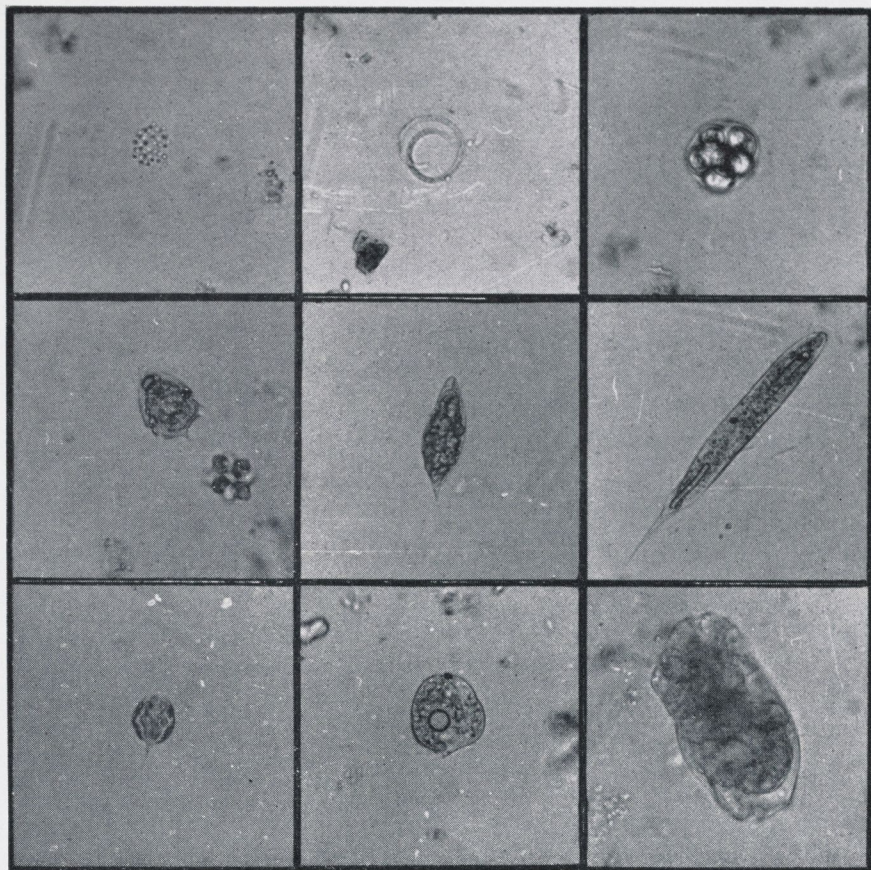


Fig. 1. Some common North Twin Lake plankters, 1955.

Top row, left to right:

- Aphanocapsa delicatissima West and West (Cyanophyta)
Anabaenopsis elenkini V. Miller (Cyanophyta)
Oocystis parva West and West (Chlorophyta)

Middle row, left to right:

- Glenodinium quadridens (Stein) Schiller (Protozoa:Mastigophora)
 (A small colony of Coelastrum microporum Naegali (Chlorophyta)
 lies just below and to the right of the Glenodinium specimen.)
Euglena gracilis Klebs (Protozoa:Mastigophora)
Euglena tripteris Dujardin (Protozoa:Mastigophora)

Bottom row, left to right:

- Phacus chloroplastes Prescott (Protozoa:Mastigophora)
Phacus acuminatus Stokes (Protozoa:Mastigophora)
Anuraeopsis fissa Gosse (Rotatoria)

(Photos by the author, 430 X enlarged three-fold)

PROTOZOA

Sarcodina

Actinopodea

Helioflagellida:

Dimorpha mutans Gruber—Fairly common in early spring (1956).

Heliozoidea:

Acanthocystis aculeata Hertwig and Lesser—Common in early spring (1956).

Actinophrys sol Ehrenb.—Common during early summer months (1954, 1955).

*Actinosphaerium eichorni Ehrenb.—Common, especially in spring and early summer. .02 (July 8).

*Heterophrys glabrescens Penard—Common during spring and early summer (1955). 0-162 (August 2-October 21).

Rhaphidiophrys sp.—Occasional occurrences in summer samples.

Rhizopodea

Amoebida:

Amoeba gorgonia Penard—Found in samples taken in early spring (1956).

Amoeba spp.—Various unidentified forms in early spring samples (1956).

Testacida:

Arcella vulgaris Ehrenb.—Occasional occurrences in summer and fall samples. 5 (September 9).

Centropyxis aculeata Stein—Uncommon to common in spring and early summer.

Clypeolina marginata Penard—Frequent occurrences in spring of 1955. 3 (June 9).

Cochliopodium bilimbosum (Auerbach)—Very common in early spring (1956).

*Diffflugia corona Wallich—Fairly common in late spring (1955).

*Diffflugia lobostoma L.—Very common, occurring in most samples. 0-36 (June 9-October 6) (Counts include other Diffflugia spp.).

*Diffflugia pyriformis Perty—Common, occurring in most samples.

*Diffflugia urceolata Carter—Occasional occurrences in plankton samples and in shad digestive tracts (1955).

*Diffflugia spp.—Includes one or two common but seemingly variable forms.

*Euglypha alveolata Dujardin—In shad gizzard (1955).

*Euglypha sp.—Very infrequent in spring and fall samples (1955). .03 (September 12).

*Pseudodiffflugia gracilis Penard—Fairly common in most samples.

- *Pseudodiffugia sp. -Common, occurring in most samples along with P. gracilis. 0-28 (June 10-October 6) (Counts include P. gracilis).
- *Trinema enchelys (Ehrenb.) -Not detected in plankton samples; found only in shad digestive tract.

Ciliophora

Euciliatia

Holotrichida:

- Cinetochilum margaritaceum Perty -Common in samples taken in early spring (1956).
- Coleps hirtus (Müller) -Common in early spring (1956).
- Cyclidium sp. -Very common, especially during the 1955 spring and early summer. 0-37 (June 9-October 21).
- Didinium nasutum (Müller) -Common in samples taken in late summer, 1954; occasional in 1955 samples. 2 (August 2).
- Holophrya sp. -Uncommon in samples taken in spring of 1955.
- Lacrymaria sp. -Occasional occurrences in 1954 summer samples.
- Mycterothrix erlangeri Lauterborn -Uncommon. Encountered in spring samples (1955). .01 (June 24).
- Paramecium sp. -Uncommon during summer months (1954).
- Pseudoprorodon sp. -In samples taken in the spring of 1955.

Spirotrichida:

- *Codonella cratera (Leidy) -Common to abundant, seemingly reaching peak production in spring and early summer. 0-15 (June 9-October 6).
- Epalxis sp. -One occurrence in late summer (1955). .01 (June 24).
- Halteria grandinella (Müller) -Common in early spring (1956).
- Stentor sp. -Very infrequent occurrences in 1955 samples. 4 (June 9).
- *Strobilidium sp. -Infrequent occurrences throughout the 1955 summer. 0-4 (June 24-August 4).
- *Strombidium sp. -Infrequent occurrences throughout the 1955 summer.

Peritrichida:

- Cothurnia annulifera Stokes -Several occurrences in samples taken in July, 1952.
- Epistylis sp. -Colonies fairly common in samples taken in spring, 1955. .01-.13 (June 24).
- *Hastatella radians Erlanger -Very common in spring and early summer, 1955. 10-24 (August 2-4); 9 (August 30).
- *Vorticella spp. -Very common in late summer and fall (1955). 10 (August 30); 0-1 (September 22-October 21).

ROTATORIA

Bdelloidea:

- *Philodina roseola Ehrenb.—Tychoplankter. Common in summer and fall (1955). 0-.09 (August 17-October 6).
Rotaria sp.—Tychoplankter. A single occurrence - in sample taken in April, 1956.

Flosculariacea:

- *Conochiloides natans (Seligo)—Common in spring and early summer (1952, 1955). .4 (June 24); .008 (August 16); 0-.36 (August 30-September 23).
Conochilus unicornis Rousselet—Uncommon; several colonies encountered in early summer (1955). .007 (June 24).
 *Filinia longiseta (Ehrenb.)—Very common in most samples; one of the six commonest rotifers. .16-2.08 (June 24-September 6); .01-.3 (September 23-October 21) (Counts include F. terminalis).
 *Filinia terminalis (Plate)—Common.
 *Pedalia mira (Hudson)—Common throughout much of the summer (1955). 0-.33 (June 24-September 12).
Pompholyx camplanata Gosse—Seemingly most abundant during the 1952 summer.

Ploima:

- *Albertia sp.¹—Identification questionable; taken in a single plankton sample (1955); common in digestive tracts of young shad (1955).
 *Anuraeopsis fissa Gosse—Very common during mid-summer, especially in 1955. 0-2.7 (August 2-October 21).
 *Ascomorpha ecaudis Perty—Uncommon, only a few individuals being observed in 1955. 0-.05 (July 8-September 14).
 *Asplanchna priodonta Gosse—Common only in late spring and early summer. 0-.24 (June 9-August 2).
 *Brachionus angularis Gosse—Very common, occasionally abundant in midsummer. .01-1.37 (June 9-October 6).
 *Brachionus calyciflorus Pallas—Very common, attaining peak abundance in early spring. 0-.42 (August 17-September 14).
 *Brachionus caudatus Barrois and Daday (f. vulgatus)—Common throughout the summer months. 0-.83 (June 9-September 23).
 *Brachionus quadridentata Hermann—Uncommon, sporadic in occurrence. .008 (August 16).
 *Brachionus urceolaris Müller—Occasional specimens observed during 1955 summer. 0-.02 (August 4-30).
Cephalodella sp.—Infrequent occurrences in 1955 samples. .008 (September 24).
 *Colurella obtusa (Gosse)—Uncommon during the 1955 summer. .02-.05 (August 16-17).
 *Dicranophorus sp.—Tychoplankter; infrequent occurrences in 1955 and 1956 samples. .01 (September 12).

¹This form is in fairly close agreement with description of Albertia given by Harring and Myers (1928).

- Euchlanis dilatata Ehrenb. -Uncommon; several specimens observed in 1954 and 1955. .004 (June 24); .026 (August 2).
- Gastropus stylifer Imhof -Fairly common in 1952 samples.
- *Keratella cochlearis (Gosse) -Very common; peak abundance is attained in spring and early summer. .09-5.3 (June-July); .008 (August 4) (Counts include next form).
- *Keratella cochlearis var. hispida (Lauterborn) -Common in spring and early summer, occurring along with K. cochlearis.
- *Keratella quadrata (Müller) -Common only in late spring and early summer. .01-.05 (June 9-10).
- *Lecane luna (Müller) -Occasional specimens observed in 1955. .01 (August 15).
- Lepadella patella (Müller) -Uncommon during the 1955 summer. .01 (August 30).
- Macrochaetus collinsii (Gosse) -Apparently rare; several specimens observed in a single sample (1955). .02 (August 16).
- Monostyla closterocerca Schmarda -Uncommon during the 1955 summer. .008 (August 2); 0-.37 (August 29-September 12).
- *Monostyla hamata Stokes -One specimen observed in shad digestive tract.
- *Monostyla obtusa Murray -Encountered only in shad digestive tracts.
- *Monostyla pygmaea Daday -A single specimen observed in shad gizzard (1955).
- *Monostyla pyriformis Daday -Fairly common in 1955 samples and in shad digestive tracts. Harring and Myers (1926) report M. pyriformis from sphagnum bogs only but the North Twin Lake specimens fit their description of this form quite accurately. .01-.1 (June 24-July 8); 0-.045 (August 16-September 23).
- Mytilina ventralis (Ehrenb.) -Uncommon; several specimens observed in 1955. .007 (June 9).
- Notholca acuminata (Ehrenb.) -Abundant but for a short period only in early spring.
- Notommatidae (Unidentified) -Several specimens observed in 1955. .007 (June 24); .025 (August 16).
- *Polyarthra major (Burckhardt) -Common sporadically. .02-3.7 (June 24-October 21) (Counts include next species).
- *Polyarthra vulgaris Carlin -Very common throughout the spring, summer, and fall months.
- Rousseletia sp. -Only one specimen observed (1955).
- Synchaeta oblonga Ehrenb. -Uncommon; most specimens were observed in 1952 and 1954 samples. .008-.02 (July 8-9).
- *Trichocerca cylindrica (Imhof) -Very common in spring and early summer. .1-5.- (June 9-October 21) (Counts include all Trichocerca spp.).
- *Trichocerca lata (Jennings) -Fairly common in spring and early summer.
- *Trichocerca longiseta (Schrank) -Common during summer months.
- *Trichocerca rousseleti (Voigt) -Seemingly very common during midsummer period.
- *Trichocerca similis (Wierzejski) -Fairly common during summer months.

*Trichocerca stylata (Gosse)—Very common during summer and early fall (1955).

*Trichocerca spp.—Includes several small species of infrequent occurrence in 1955 samples.

Eggs of rotifers were found in plankton from June 9–October 21. Numbers ran as high as 42 per milliliter.

ARTHROPODA

Crustacea

Branchiopoda

Cladocera:

*Bosmina longirostris (O. F. M.)—Very common in late spring and early summer; one of the commonest of the Cladocera. .02-.4 (June-July); 0-.01 (August 2-30).

*Ceriodaphnia pulchella Sars—Common in late spring (1955).

*Ceriodaphnia quadrangula (O. F. M.)—Common in late spring, early summer, and fall. 0-.03 (June 24-August 30).

*Chydorus faviformis Birge—A single specimen noted in shad gizzard (1954).

*Chydorus sphaericus (O. F. M.)—Very common during summers of 1951, 1952, and 1953; fairly common in 1954 and conspicuously absent in 1955; in shad gizzards (1954).

*Daphnia longispina (O. F. M.)—Very common, especially in late spring and early summer; one of the principal foods of very young game and pan fishes. 0-.16 (June 10-July 9).

*Daphnia pulex (deGeer)—Common, occurring with D. longispina in spring.

*Diaphanosoma brachyurum (Lievin)—Common in 1952 net plankton samples.

Leptodora kindti (Focke)—Uncommon in plankton samples; occasional specimens found in fish stomachs.

*Leydigia quadrangularis (Leydig)—Not taken in plankton samples; occasional specimens found in fish stomachs.

Macrothrix laticornis (Jurine)—Fairly common in late spring and early summer.

*Moina micrura Kurz—Especially common during the 1955 summer when it constituted one of the principal foods of young game fishes. .01 (June 9); .01-.03 (August 30).

Polyphemus pediculus (L.)—Occasional specimens found in fish stomachs.

Scapholeberis mucronata (O. F. M.)—Not taken in plankton samples. Several specimens found in stomachs of small fish in 1954 and 1955.

Ostracoda

*Cypria obesa Sharpe—Tychoplankter (occasional); not taken in plankton samples; occasionally present in food of small fish.

*Cypridopsis vidua (O. F. M.)—Not taken in plankton samples; several occurrences in food of small fishes.

Copepoda

Eucopepoda:

*Cyclops bicuspidatus Claus—Common to abundant; including its larval stages, this form is the most common of the planktonic Crustacea. (This was the only species of Cyclops detected in the North Twin Lake samples.) .003-.079 (June-July); 0-.015 (August 2-29).

*Diaptomus oregonensis Lillj.—Common to abundant only for rather brief periods in late spring and early summer. .016-.053 (June); 0-.015 (August 2-20).

Orthocyclops modestus (Herrick)—Littoral form; occasional occurrence in 1955 samples.

Paracyclops fimbriatus (Fisher)—Tychoplankton; occasional occurrence in 1955 samples.

Nauplii were observed on many occasions. .06-.22 (June-July); 0-1.15 (August 2-October 21).

Arachnoidea

Hydracarina:

*Limnochares sp.—Adventitious plankton not taken in plankton samples but frequently found in fish stomachs.

*Unidentified larvae—Tychoplanktonic; occasional occurrences in 1955 samples. .008 (August 17).

Insecta

Collembola:

*Podura aquatica L.—Tychoplanktonic; not taken in plankton samples but found in shad digestive tract (1955).

Diptera:

Ceratopogonidae (larvae)—Adventitious plankton of very infrequent occurrence in 1955 samples.

*Chaoborus punctipennis Say (Larvae: early instar)—Very infrequent plankton. .008 (August 16).

*Tendipedidae (Unidentified larvae)—Adventitious plankton of very infrequent occurrence in 1954 and 1955 samples. .004 (June 24); .008 (August 16); .008 (September 16); .01 (October 6).

MISCELLANEOUS PLANKTON FORMS

ANNELIDA

Oligochaeta:

Aelosoma variegatum Vejd.—Tychoplanktonic; one or two occurrences in 1954 samples.

NEMATODA

Unidentified—Frequent occurrences in samples taken during the 1955 summer. .004 (June 24; 0-.03 (August 2-September 16).

BRYOZOA

*Plumatella sp. (Statoblasts)—Occasional occurrences in 1954 and 1955 samples. 0-.03 (August 29-September 12).

In general, zooplankton constituted a relatively small portion (15.7 per cent) of the total North Twin Lake plankton volume during the 1955 study period (Table 2). Such an occurrence is about what would have been expected for this period, i.e., that the producers (phytoplankton) be volumetrically in excess of the consumers (zooplankton) which they support. Such results are rarely obtained in studies involving net plankton only, where the bulk of the consumers usually exceeds that of the producers. This problem has been the concern of limnologists for many years (e.g., Rawson, 1956a) and it is generally agreed that the apparent fallacy is due to the inability of the net to retain the usually abundant nannoplankton. Refined plankton sampling techniques such as the centrifuge or sedimentation methods offer practical means for avoiding such pitfalls.

Amoeboid and ciliate Protozoa were important components of the North Twin Lake zooplankton during most of the study period but like the remainder of the zooplankton, comprised little of the total plankton volume. Of the Sarcodina, the actinopod, Heterophrys glabrescens, and rhizopods, Diffugia spp. and Pseudodiffugia gracilis, were the important forms. Diffugia spp. were consistently the most frequently occurring of these forms.

Relatively speaking, ciliates did not attain the same degree of importance on a volumetric basis as did the Sarcodina although Codonella cratera occasionally approached such a position. Other ciliates that reached measurable proportions in the plankton at various periods were Hastatella radians in early August, Cyclidium sp. throughout the late summer, and Vorticella sp. in late October.

Except for the month of June, Rotatoria consistently made up the bulk of the zooplankton encountered in the samples. Considered collectively, they comprised 54.9 per cent of the zooplankton volume and 8.6 per cent of the total plankton volume (Table 2). Species of five genera more or less dominated the rotifer populations at practically all times. These genera were Anuraeopsis, Brachionus, Filinia, Polyarthra, and Trichocerca. Considered from the standpoint of their bulk and the frequency with which they occurred in samples during the study period, the principal species were Anuraeopsis fissa, Brachionus angularis, B. caudatus, Filinia longiseta, Polyarthra vulgaris, Trichocerca longiseta, T. rousseleti, and T. stylata. Several of these rotifers were described by Carlin (1943) as typical summer forms. Other species attained significant proportions for relatively short periods at various times during the season. For example, Asplanchna priodonta, Keratella cochlearis,

Trichocerca cylindrica and T. lata seemed to be the important forms during the month of June. Brachionus calyciflorus, Conochiloides natans, and Notholca acuminata are very common at even earlier periods as was revealed by the analysis of several samples obtained in March and April of 1956.

Cladocera and Eucopepoda did not contribute measurably to the plankton except during the early stages of the study. At this time, Bosmina longirostris, Daphnia longispina, D. pulex, Cyclops bicuspidatus and Diaptomus oregonensis were the important forms. Their frequent occurrence in the digestive tracts of fish collected during this period further substantiated the relative magnitude of their abundance.

It is believed, however, that the plankton Crustacea were not as adequately sampled as might have been desirable. Although their relative abundance is usually low compared to that of most other plankters, they nevertheless constitute upon occasion an important segment of the total plankton volume and should be measured as accurately as possible. The acquisition of larger water samples would have undoubtedly reduced the sampling error and, consequently, the errors associated with estimating the volume of these bulkier but less numerous organisms. Better volumetric estimates of these forms would quite likely have lowered the phytoplankton-zooplankton (p:z) ratio somewhat although it is felt that the reduction would not have been appreciable.

Fairly well documented is the fact that in many waters planktonic crustacean production declines markedly during the hot summer months. Such was the case at North Twin Lake during the 1955 summer even though it is acknowledged that the sampling procedure followed may not have been as efficient in capturing these large zooplankters as would have been desirable. Analyses of fish digestive tract contents (including those of gizzard shad) suggested that fairly good populations of Cladocera and Eucopepoda existed even when plankton sample analyses failed to reveal their presence. However, the fact that the fish examined may have selected or actually sought out these forms more or less precludes making statements concerning abundance of these plankters based upon their incidence in the fishes' food.

It seems worth mentioning here that the analyses of the several samples obtained in March and April, 1956, employing exactly the same method used in 1955 also indicated that Cyclops bicuspidatus was the dominant zooplankter during the early 1956 spring. Furthermore, it is significant to note that computed p:z ratios for these samples were slightly in favor of the zooplankton. Hence, on the basis of these findings, it might be concluded that most samples obtained and analyzed by the methods described earlier are fairly representative even though they may not appear to be at first glance.

SUMMARY

In summarizing, it might be pointed out further that the series of samples taken from North Twin Lake employing the centrifuge method of concentration have lucidly exhibited from both numerical and volumetric standpoints the typical annual phyto-zooplankton production cycles,

namely, high zooplankton and comparatively low phytoplankton development in early spring followed by a sharp decline in zooplankton production and high phytoplankton development during the summer.

The tripton or planktonic abioseston was usually present in fairly large amounts, its bulk averaging about three times that of the planktonic bioseston.

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The Fern Lake Trace Mineral Metabolism Program

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ABSTRACT

The role of the mineral supplements in the management of fish ponds, game ranges, and forests has been a research subject of a host of individuals and organizations for many years. Nearly all of such projects, however, have been limited by analytical techniques that can at best be applied only to the macronutriments.

The cooperative program at Fern Lake, conducted by the U. S. Atomic Energy Commission, University of Washington and the State of Washington Department of Game, embraces studies in which the total mineral need in the ecology of the Fern Lake watershed is evaluated by the use of the techniques of the radiation biologist. Using the combined skills of the physical and biological sciences it is hoped that great progress can be made in improving the productive capacity of this impoverished watershed.

INTRODUCTION

The productive capacity of land and water areas has been the subject of investigation by many agencies and thousands of individuals for many years. Mortimer and Hickling (1954) have abstracted 351 research papers on the role of fertilizers in fishponds. The literature on artificial fertilization of lakes and ponds also was reviewed by Maciolek (1954). In forestry and farm journals repeated reference is made to the need for adding deficient elements to the soil. White and Leaf (1956) list 235 scientific periodicals in which articles on forest fertilization are published. However, in spite of the many years of effort expended on the study of the methods of application of fertilizers to land and water areas and the results obtained, there remain numerous problems to be solved, especially in the mineral-deficient, rain-leached northwest coastal region of the United States.

In 1957, studies for the trace mineral metabolism program at the Fern Lake laboratory were initiated in an attempt to apply the accumulated knowledge to the improvement of the pro-

ductive capacity of land and water resources, and, through cooperative effort, to develop methods and practices which would maintain the environment by retarding "the downhill flow of nutrients from the hills to the sea" (Leopold, 1941) and accentuate the uphill movement of nutrients by natural and artificial means.

It was realized that a number of scientific disciplines and administrative agencies could contribute to the accomplishment of the broad objectives of the program. Thus, the University of Washington, the Washington State Department of Game and the U. S. Atomic Energy Commission, by pooling resources and scientific personnel in a cooperative team effort, have and are making a positive contribution to the progress of the program.

In organizing the research effort for the Fern Lake laboratory, the University of Washington, under the general supervision of the Dean of the Graduate School, provides the laboratory facilities and scientific skills for a portion of the program; the Washington State Department of Game has made available the lake and its watershed as well as the necessary buildings and the essential management experience; and the U. S. Atomic Energy Commission provides financial support, special equipment and skills in the new methods of isotopic research.

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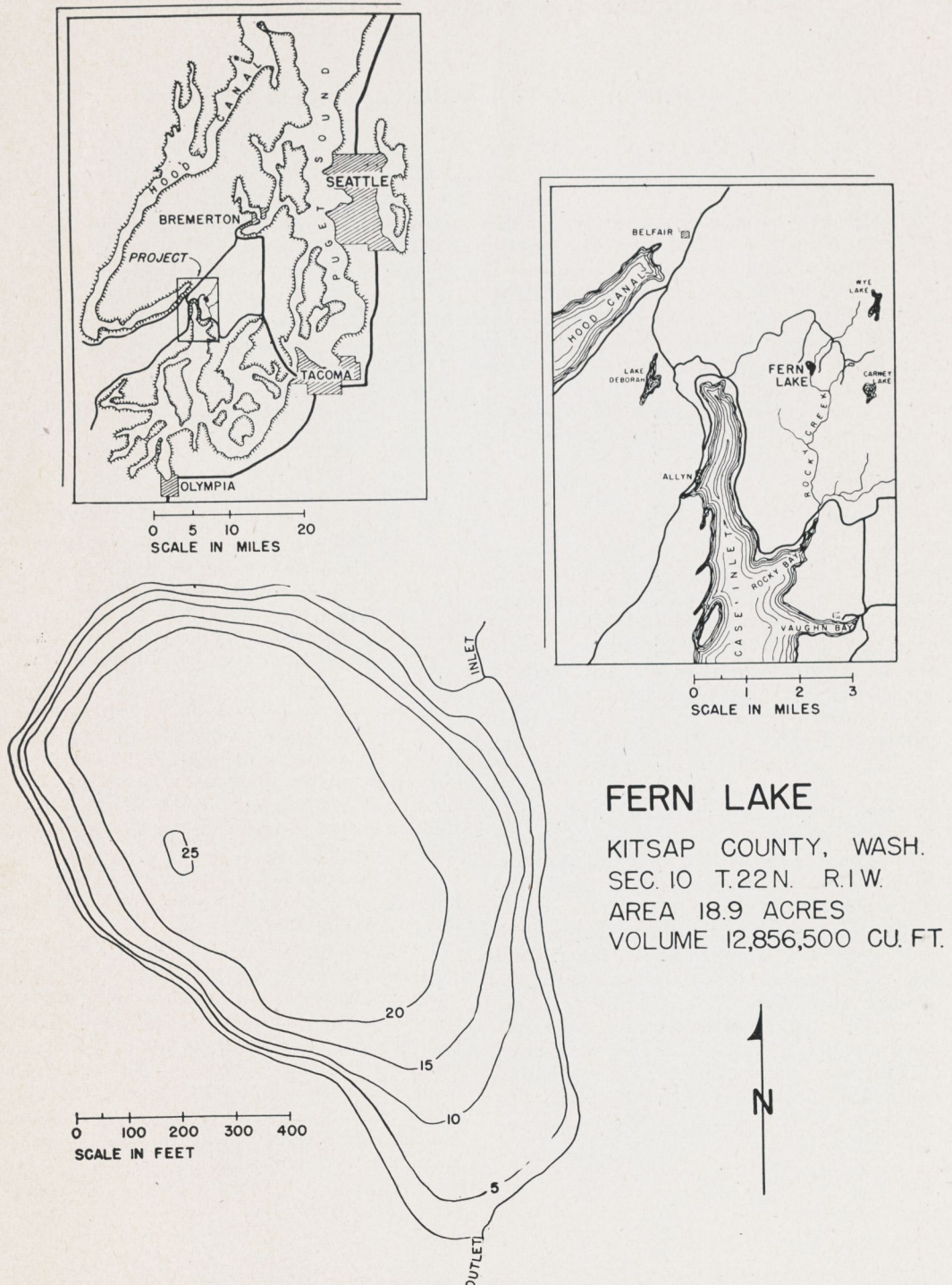


FIGURE 1.—Map of Fern Lake and environs.

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TURNOVER TIME AND PRODUCTION OF PLANKTONIC CRUSTACEA IN LIMED
AND REFERENCE PORTION OF A BOG LAKE

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INTRODUCTION

Bog lakes may be compared to engines which have operated on low-quality fuel and have, as a consequence, lost efficiency in the conversion of energy. Treatment of such lakes with hydrated lime provides at least a measure of temporary correction as inferred by the appearance of algal blooms (Waters 1957) and larger standing crops of zooplankton (Johnson and Hasler 1954, Waters and Ball 1957). The mechanisms by which alkalinization augments production have been reviewed elsewhere (Stross and Hasler 1960).

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The observed increases in standing crops of primary consumers following treatment is presumed to reflect an increase in production at this trophic level. If the assumption is correct, there is, as yet, no good evidence that the increase is transferred to the plankton consumer. Johnson and Hasler found no increase in production of rainbow trout, a secondary consumer in early life, in a lake treated with lime despite the observed increase in the standing crop of *Daphnia*, the chief source of food for the trout in the lake. They attributed a part of the failure to reduced utilization resulting from dilution of food following a lime-induced increase in depth of the aerobic zone

of the lake. The susceptibility of trout to stress when competing with other members of the same species (Brown 1957) also may have been responsible for the failure of the trout to respond to the presumed increase in production of food. In view of the inconclusive circumstantial evidence, it became of interest to attempt a direct measurement of production at the level of primary consumers.

Measuring production of the planktonic Crustacea, the primary consumers, was made feasible with the help of 2 simplifications. It was assumed first, that an average standing crop was being replaced at a constant rate, and, second, that the rate of replacement of all species represented was approximately the rate of replacement of the dominant species. Because *Daphnia* dominated both portions of the lake, it was selected for this determination. The choice was facilitated by the fact that growth is proportional to the quantity of food available (Slobodkin 1954, 1959).

THE LAKE

The use of Peter-Paul Lake was appropriate for a comparative study because of the treated (Peter) and untreated portions (Paul). In 1951 Peter-Paul Lake (T45N, R8E, S36; Gogebic Co., Mich.) connected originally by a narrow, shallow channel, was separated with earth being used to fill the connection. Following the separation, Peter Lake (6 acres) received treatment with about 6.5 tons of hydrated lime over 3 years. The portion known as Paul Lake (3 acres) was preserved as a control.

Measurements of the physical and chemical characteristics of the water in the treated portion showed an increase in transparency, pH, and ions contributed by hydrated lime. During the 3-year period of the study the epilimnion and euphotic zone were about 50% deeper in the treated part. The zone inhabited by planktonic Crustacea was double that of the control as a result of an increase in depth of the aerobic layer. In the epilimnion pH was increased from 6.4 to 7.2. Alkalinity was increased by a factor of 3.0, calcium by 2.5 and magnesium by 6.0. There appeared to be no decline in the above values during 1955 and 1956, two years after treatment was discontinued. If regression in the chemical environment occurred, there was no evidence of it in the indices selected for measurement. A fuller description of morphology and results of lime treatment are reported elsewhere (Stross and Hasler 1960).

METHODS

Collections of planktonic Crustacea and analysis of the samples were made in a conventional manner. Horizontal tows with the Clarke-Bumpus

sampler were made over a circular course around the center of the lake and throughout the zone inhabited by the planktonic Crustacea at depth-intervals of one meter. Replicate samples were taken with each of mesh-sizes 2 and 10 bolting silk (0.37 and 0.16 mm i. m. d., respectively). Because the number of samples became cumbersome with this procedure, the method of Edmondson (1955) was employed during the final year and consisted of lowering and raising the sampler (#10 mesh attached) with a uniform motion while the boat circumscribed the course at uniform speed. Samples taken in the horizontal tows were strained from an average of 800-900 liters of water, and those in the composite sample (#10-mesh net), from 300-400 liters. Such collections were made from early May to mid-November, or during the ice-free period, and intensively from mid-June to late September. Samples were collected at time-intervals of 2 weeks in 1954, and of approximately 10 days in 1955. In 1956 the composite samples, which were used for determining turnover time, were collected each day and the horizontal tows, each week. All samples were preserved in an ethanol solution.

Numerical analysis consisted of counting the individuals of each species in three 1-ml aliquots which were taken from each of the 2 replicates. Weights were obtained from samples dried at 60°C and desiccated for 24 hours. Collections from the number-2-mesh nets were used because of their virtual freedom from contamination with rotifers and colonial algae.

Categorization of Daphnia according to size-age

In the enumeration procedure *Daphnia* were classified into 6 arbitrarily designated size categories, 3 postnatal and 3 embryonic groups, after the method of Slobodkin (1954). Separation of individuals into the postnatal categories was as follows: Adults included all individuals equal to or larger than the smallest individuals containing eggs or embryos in the brood pouch. The division of the 2 immature stages was, likewise, arbitrary, the minimum size of the intermediate or youthful stage being in accord with the minimum size of the adults under the assumption that the factors(s) governing growth of all postnatal instars had the same effect on all. The 3 embryonic stages were: (1) eggs fully swollen to the formation of fat droplets, (2) eggs showing cleavage to the formation of a pigmented eye-spot, and (3) embryos with eye spots until birth, or if the embryo had dropped from the brood pouch, until it resembled instar I. These stages were similar to those used by Edmondson (1955) except that stage I was of shorter duration than that given by Obreskove and Fraser

**The effect of mineral fertilizers on the growth of trout
in some Scottish lochs**

W. R. MUNRO (Pitlochry, Scotland)

With 2 figures and 2 tables in the text and on 1 folder

Little is known about the effect of fertilizers upon the growth rate of brown trout in natural lakes. FROST and SMYLY (1952) could show no clear-cut benefits following enrichment with bonemeal. In Australia, WEATHERLEY and NICHOLLS (1955) recorded an improvement in growth rate following additions of a mixed chemical fertilizer (NPK+Ca).

An investigation into the effects of two types of mineral fertilizer on trout growth was started in 1954 in five small lochs in north-west Scotland. These lochs were chosen because they contained natural populations of small, slow-growing, brown trout. Later results suggested that in two of these lochs some juvenile sea trout were also present. Brief details of the physical and chemical characteristics of the lochs studied are given in table 1.

Table 1. Physical and chemical characteristics of the lochs.

Loch	Area		Mean depth		pH*	Alkalinity* mg CaCO ₃ /l
	Acres	Hectares	Feet	Metres		
Mhullaich	9.1	3.68	9	2.74	6.8	4.4
Smuraich	5.9	2.39	15	4.57	5.7	1.0
Beiste Brice	6.8	2.75	11	3.35	6.8	5.2
Grosvenor	6.2	2.51	10	3.05	5.8	2.0
Daimh Mhor	20.4	8.25	13	3.96	7.3	11.8

* Before fertilization.

Loch Mhullaich was selected as a control and remained untreated throughout. The other lochs received two applications of phosphatic fertilizer in 1954 and three in 1955. In addition, the two most acid lochs received a single application of ground limestone in 1954. Details of the treatments are given in table 2.

These applications resulted in considerable temporary increases in the phosphorus content of the water and in the pH and alkalinity of those lochs which received limestone (HOLDEN 1959). These chemical changes were accompanied by qualitative changes and quantitative increases in the micro-flora and by increases in the weight of the standing crop of bottom fauna in the two lochs examined quantitatively.

Table 2. Total additions of fertilizers 1954—1955.

Loch	Treatment	Total weight added in lbs/acre (kg/hectare)			
		N	P (Soluble)	K	CaCO ₃
Mhullaich	Untreated control	—	—	—	—
Smuraich	NPK + CaCO ₃	62.0 (69.4)	24.2 (27.1)	31.0 (34.7)	1139.0 (1275.7)
Beiste Brice	NPK	53.0 (59.4)	20.3 (22.7)	26.1 (29.2)	—
Grosvenor	Superphosphate + CaCO ₃	—	20.3 (22.7)	—	1084.0 (1214.1)
Daimh Mhor	Superphosphate	—	23.7 (26.5)	—	—

The trout populations were sampled with gill nets before the first application. Later in 1954 and thereafter samples were taken by shore-seining or angling. With the exception of the gill-net samples all the fish were released after samples of scales had been taken and they had been measured and, in most cases, weighed.

Ages have been estimated from the scales and the lengths of the trout at the end of each year of life calculated. Before fertilization the characteristics of the trout in these five lochs were very similar. They were short-lived, none reaching an age greater than 5+, and their growth rates were such as might be expected in oligotrophic lochs.

It is only possible here to give an outline of the observations made on the growth rates of the trout during the experiment. Details of growth rates for several years before fertilization are available but in this account the calculated lengths for 1953 have been taken as typical. Fig. 1 shows the increase or decrease in the calculated lengths for 1954 to 1957 when compared with the 1953 values (five-years-old fish are omitted).

In Mhullaich, the untreated control loch, the trout were slightly larger age for age in 1954 than 1953, but the annual variation from the 1953 values has been small and has shown no distinct trend.

In all the treated lochs there was an improvement in the size of the trout following fertilization, but the timing of its appearance and its duration has differed in the various lochs. In general there was little effect on first year calculated lengths, while the initial effect was most marked on two-year-olds. However, as might be expected, after two or more years of improved growth the older fish showed the greatest increase in length. Conversely, the calculated length for two-year-old fish were the first to return to pre-fertilization levels when the benefits of fertilization ceased.

In Smuraich (NPK+Ca) there was an immediate response to fertilization, the calculated lengths for 1954 being from 2 to 4 cm. greater than the corresponding values for 1953. In 1955 this improved growth rate continued and resulted in a further improvement in the size of the fish and up to 1957 this improvement in size was largely maintained, while samples taken in 1958 indicated that the final values for 1958 will again be well above those before fertilization.

In Beiste Brice (NPK) there was also an immediate response to fertilization in 1954 with similar increases in the calculated lengths. In May 1955 a phytoplankton bloom developed and reached a peak in August, with a density of about 60 million cells/litre, when the water was almost opaque. A bloom appeared again in 1956 but it was never so dense as in 1955. Samples of trout taken during the bloom in 1955 revealed that the fish were not growing as well as in 1954, although mainly due to the length increases made in that year, the 1955 calculated lengths were still considerably better than those for 1953. In 1956, after the disappearance of the bloom, the improved growth rate was not resumed and by 1957 the calculated lengths had almost returned to their original level, only the oldest fish still showing the benefits of the initial improvement.

There was also an improvement in the growth rate in 1954 in Grosvenor (P + Ca) and the proportionate increases in length were comparable to those of the trout in the two preceding lochs. This improved growth was maintained in 1955, but in 1956 and 1957, the return of the calculated lengths of the younger fish towards their level before fertilization suggests that the benefits of the fertilizer are almost exhausted in this loch.

In contrast, in Daimh Mhor (P) the 1954 calculated lengths for all age groups except two-year-olds were smaller than those for 1953. Again in 1955 there was little sign of a general improvement in growth rate and it was not until 1956 that a marked change in the growth rate occurred, producing increases in the calculated lengths comparable with those experienced earlier in the other lochs. The improved size of the fish was maintained in 1957, while samples taken in 1958 indicated that the calculated lengths for that year will again be well above pre-fertilization levels.

The calculated lengths so far considered show quite clearly that improvements have followed fertilization but they do not emphasise the extent of the improvement. Since the weight is approximately proportional to the cube of the length, a comparatively small increase in length represents a significant increase in weight, particularly in the larger fish. Examples of the weight increases following fertilization are given in Fig. 2 where the increase or decrease in the average weight for each age group in the spring samples for 1955—1958 are shown as a percentage of the corresponding weights for the spring sample in 1954, before fertilization. There was also a tendency for the coefficient of condition ("K") of the older fish to be higher where they had shown improved growth.

The results of these experiments demonstrate that in these oligotrophic lochs improved growth rates resulted from the addition of mineral fertilizers but there appears to be no distinct difference between the improvements in growth rate produced by the two phosphatic fertilizers.

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FIG. 1. DECREASE OR INCREASE IN CALCULATED LENGTH

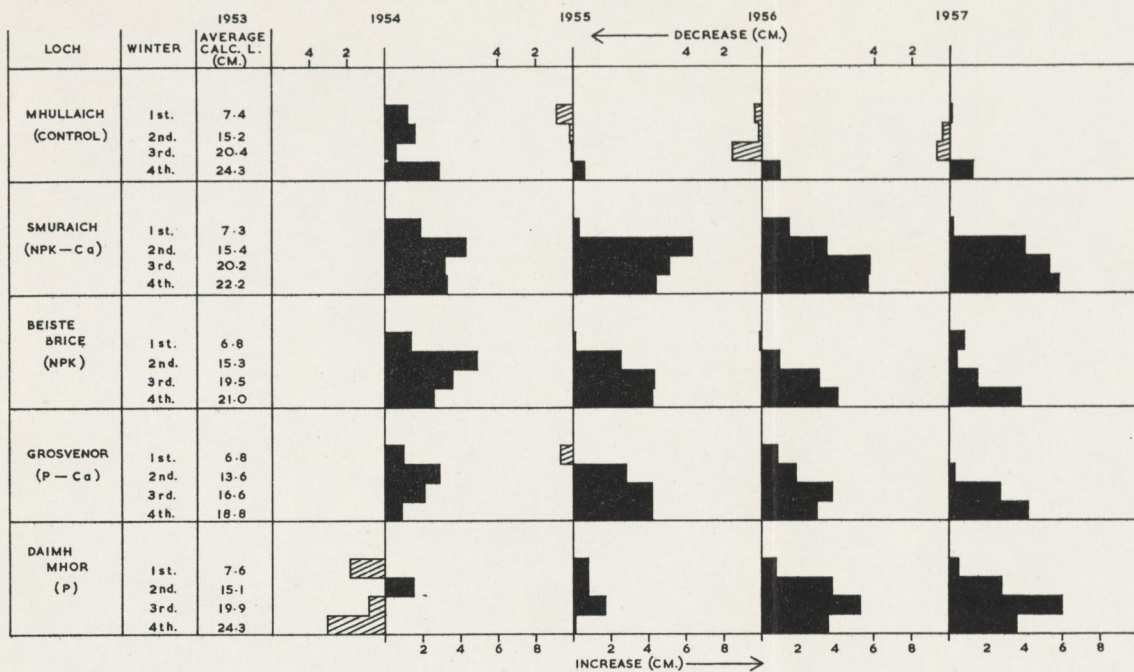
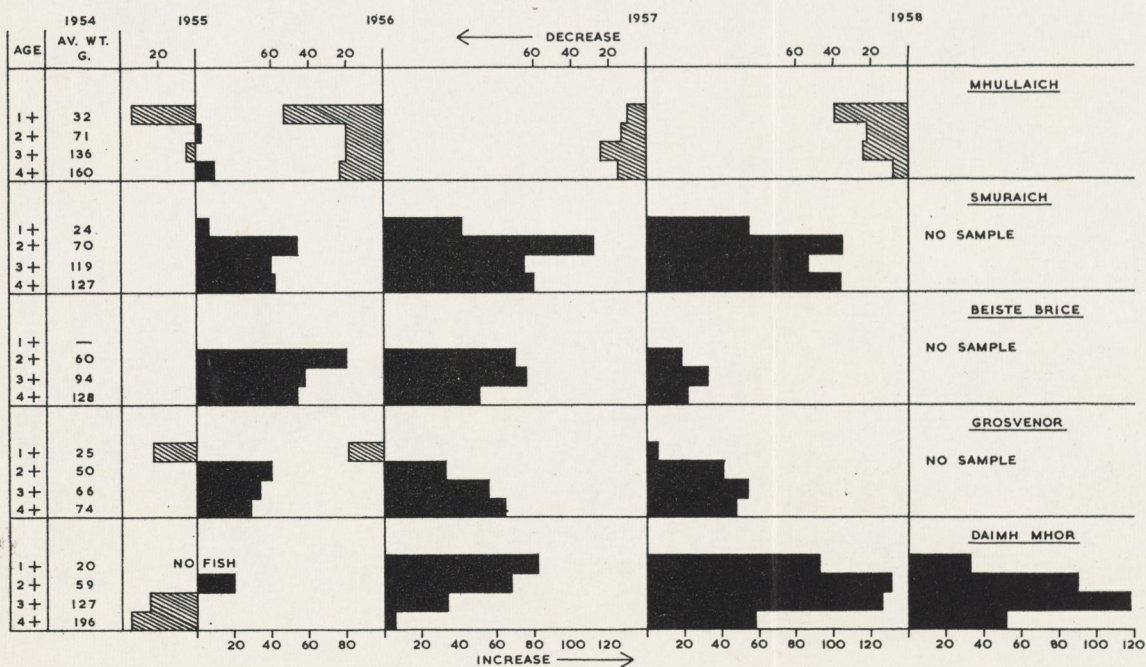
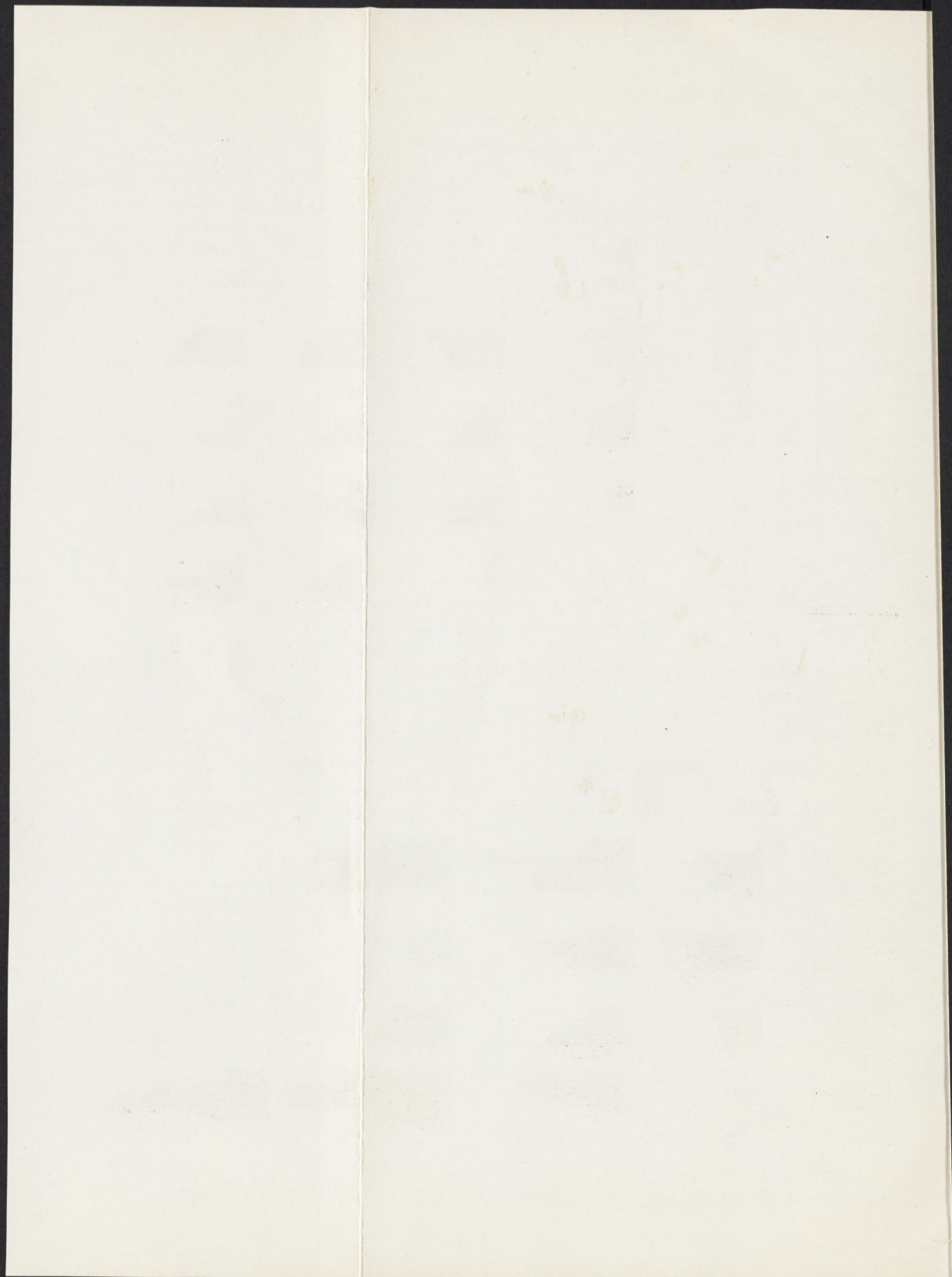


FIG. 2. PERCENTAGE DECREASE OR INCREASE IN WEIGHT





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Discussion

HASLER: Were there unusual mortalities from disease, fish-eating birds and mammals which would have reduced the population and hence made more food available for remaining fish?

MUNRO: There was no evidence of unusual mortality due to disease or to predation which could have reduced the population density and affected the growth rate.

HAYES: Was there any estimate of the total biotic mass at the fish trophic level, during the experiment? It would seem difficult to estimate the effect of fertilization without bringing this term into the equation. Increase in young stock or cannibalism could affect the conclusion.

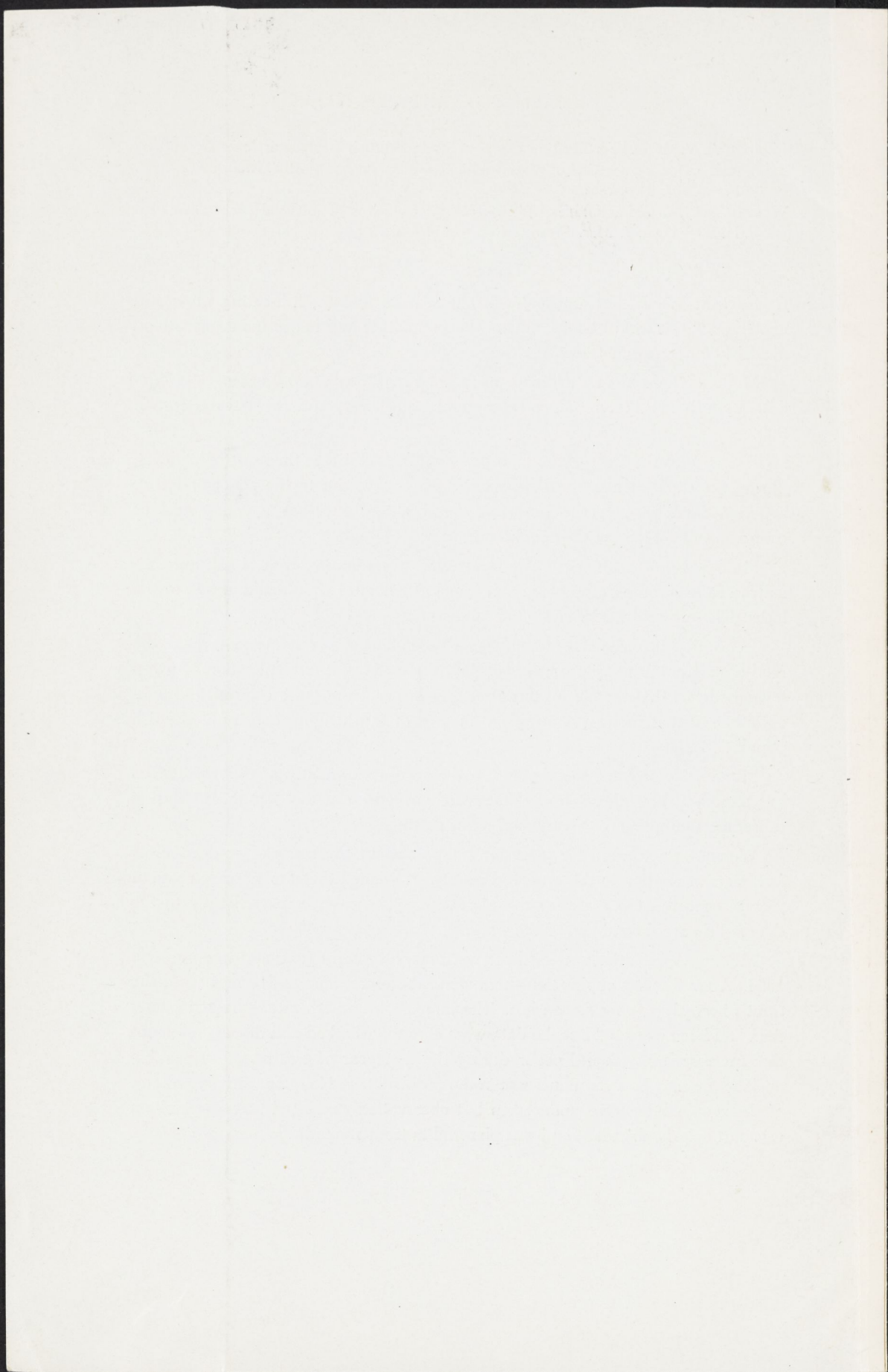
MUNRO: No attempt was made to estimate the standing crop of fish but estimates of the standing crop of bottom fauna of the mud were made in two of the lochs. These showed a 12 to 18-fold increase.

JOHNSON: Your presentation implies an increased transfer of energy through the food-chain from primary producers to the trout as a result of fertilization. Do you have evidence that the size of the trout populations were quite constant throughout; that is, that there was no effect on growth by changing density of the fish populations?

MUNRO: No attempt was made to make accurate estimates of the populations but there was no indication of changes in the density of the populations during subsequent sampling, either by angling or netting.

WORTHINGTON asked for more information about the times of application of fertilizers in relation to the observed results. It seemed that the increased rate of growth occurred too early for the biological cycle to have reacted fully to the changed chemical condition of the water.

MUNRO: Applications of fertilizer were made in early June and in August in 1954. After the first application there were, therefore, four to five months of the trout's normal growing season left. The increase in growth rate appeared sooner than had been expected but the data were carefully checked and there is no doubt that increased growth did occur during the first year of treatment. A possible explanation may be a rapid increase in the zooplankton. No quantitative estimates of the zooplankton were undertaken but observation suggested that zooplankton was particularly abundant and was plentiful in trout stomachs.



To Dr. P. R. Needham

[1961]

with kind regards

P. M. Jónsson

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**Population dynamics in *Chironomus anthracinus* Zett.
in the profundal zone of Lake Esrom**

PÉTUR M. JÓNASSON (Hillerød, Denmark)

With 6 figures in the text and on 2 folders

Introduction

Productivity studies, mainly on bottom faunas, have been carried out on Lake Esrom (Esrom Sø) (North Zealand, Denmark) since 1953. The present investigation forms part of these studies.

Studies on freshwater productivity are usually concerned with plankton, in particular phytoplankton, and fish and few, if any, have been based on the bottom fauna. On the other hand the standing crop of bottom fauna has been studied repeatedly (e. g. EKMAN 1915, JUDAY 1922, OLSTAD 1925, LUNDBECK 1926, VALLE 1927, RAWSON 1930, LANG 1931, BERG 1938, DEEVEY 1941 and BRUNDIN 1949). The bottom fauna serves as food for fish and is, therefore, one of the main links in the food chain of a lake. The yield of bottom invertebrates per unit of time is thus of both scientific and practical interest. One of the most successful attempts to measure it was made by BOYSEN JENSEN (1919) for the plaice-feeding areas of the brackish waters of Limfjord, Denmark.

The present study required a locality of great area, with uniform ecological conditions, and inhabited by only few species. Such conditions prevail in the profundal zone of Lake Esrom.

Physiographical notes

Lake Esrom (fig. 1) has been described by BERG (1948) and by JÓNASSON and MATHIESEN (1959). Fig. 2 shows a transverse section of the lake, its temperature and oxygen content. The bottom of the lake below about 10 m is covered with mud. A comparison between the morphometry of the basin (Fig. 1) and temperature and oxygen content (Fig. 2) shows that throughout extensive areas of the lake (10 sq. km) the bottom temperature is less than half the surface temperature during July—November (cf. Fig. 3). During this period the oxygen content in the bottom layers is so low that only a few species are able to survive.

The fauna of the profundal zone

Oligochaeta	Tubificidae	<i>Tubifex tubifex</i> (O. F. MÜLLER) <i>Tubifex barbatus</i> (GRUBE) <i>Ilyodrilus hammoniensis</i> MICHAELSEN
Cladocera		<i>Iliocryptus agilis</i> KURZ

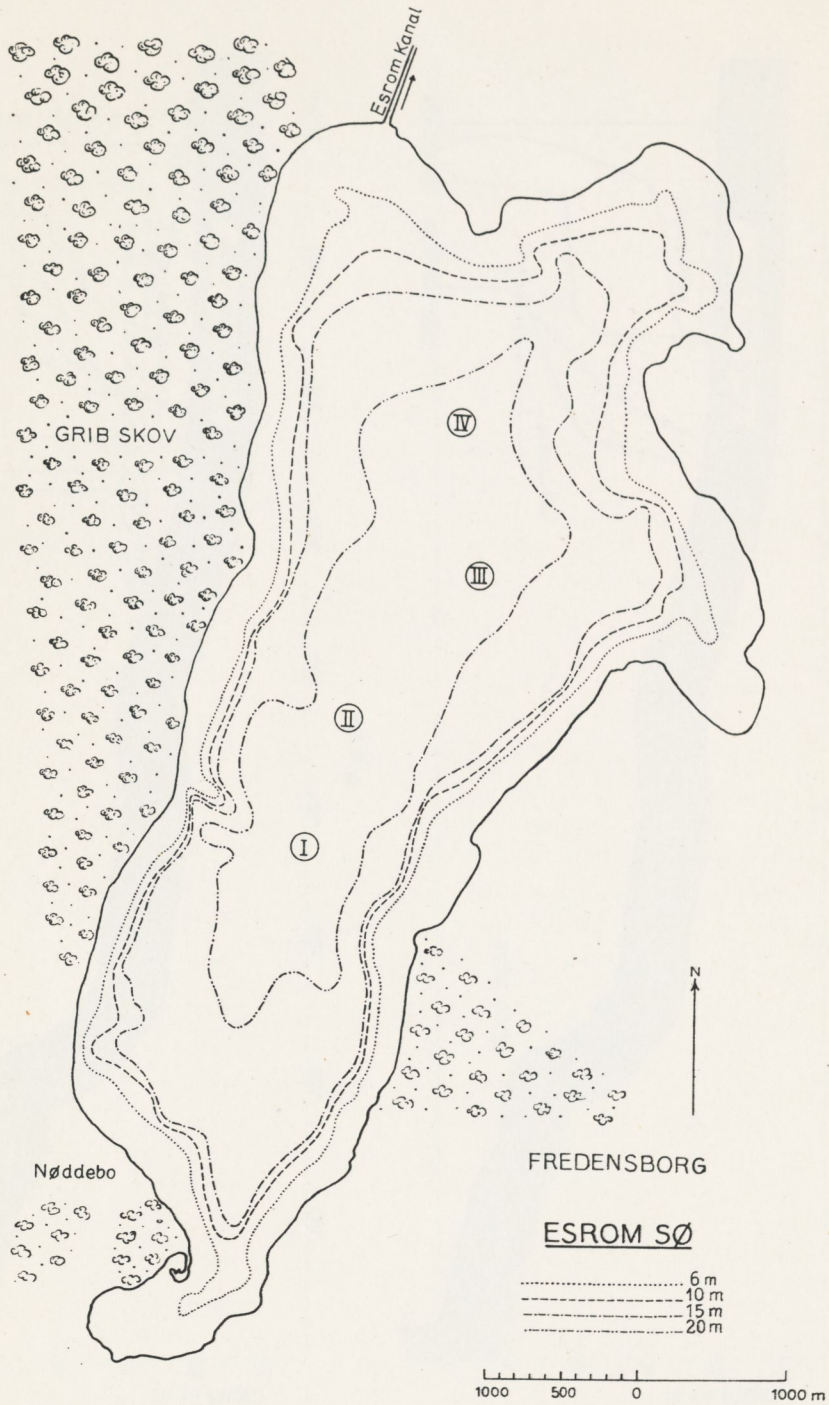
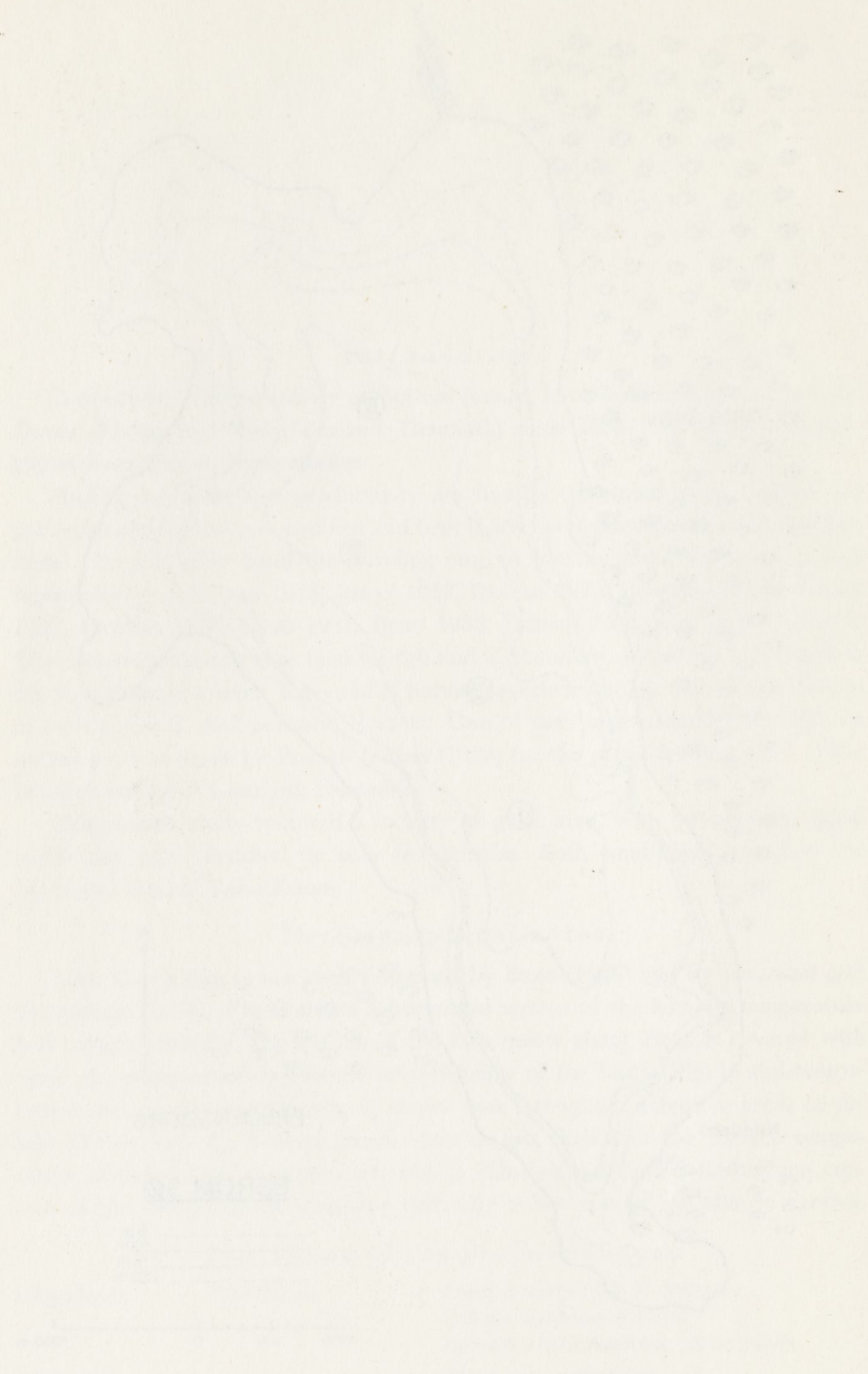


Fig. 1. Bathymetric chart of Lake Esrom.

P. M. Jónasson: Population dynamics in *Chironomus anthracinus* ZETT.



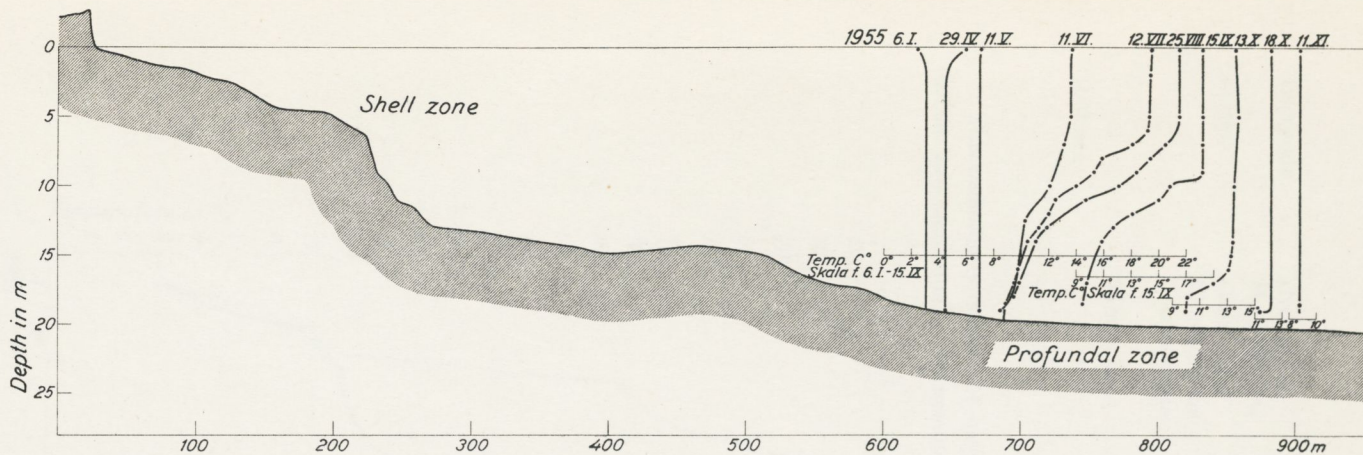


Fig. 2 a.

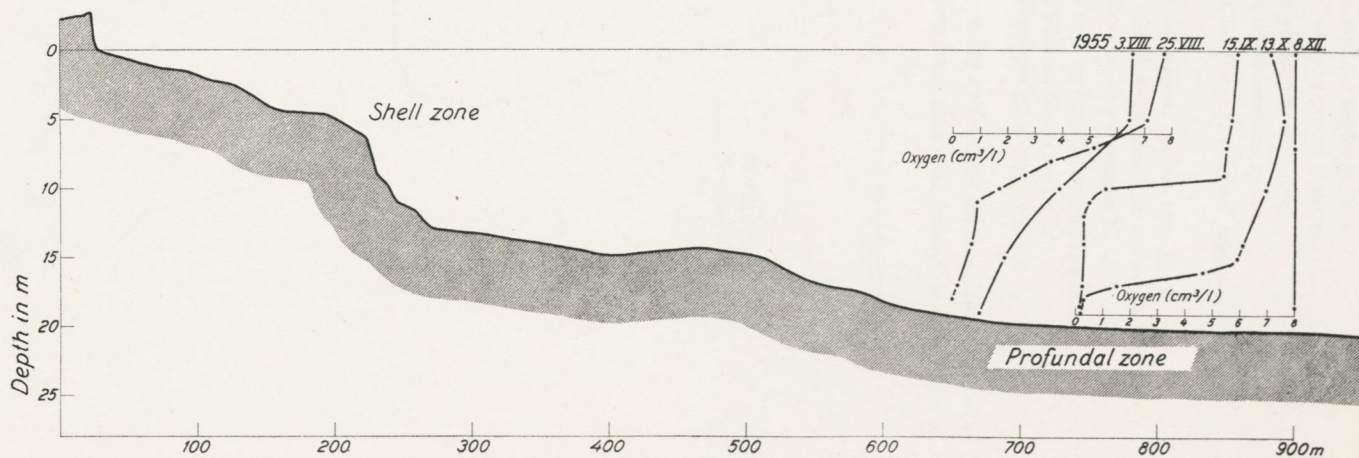
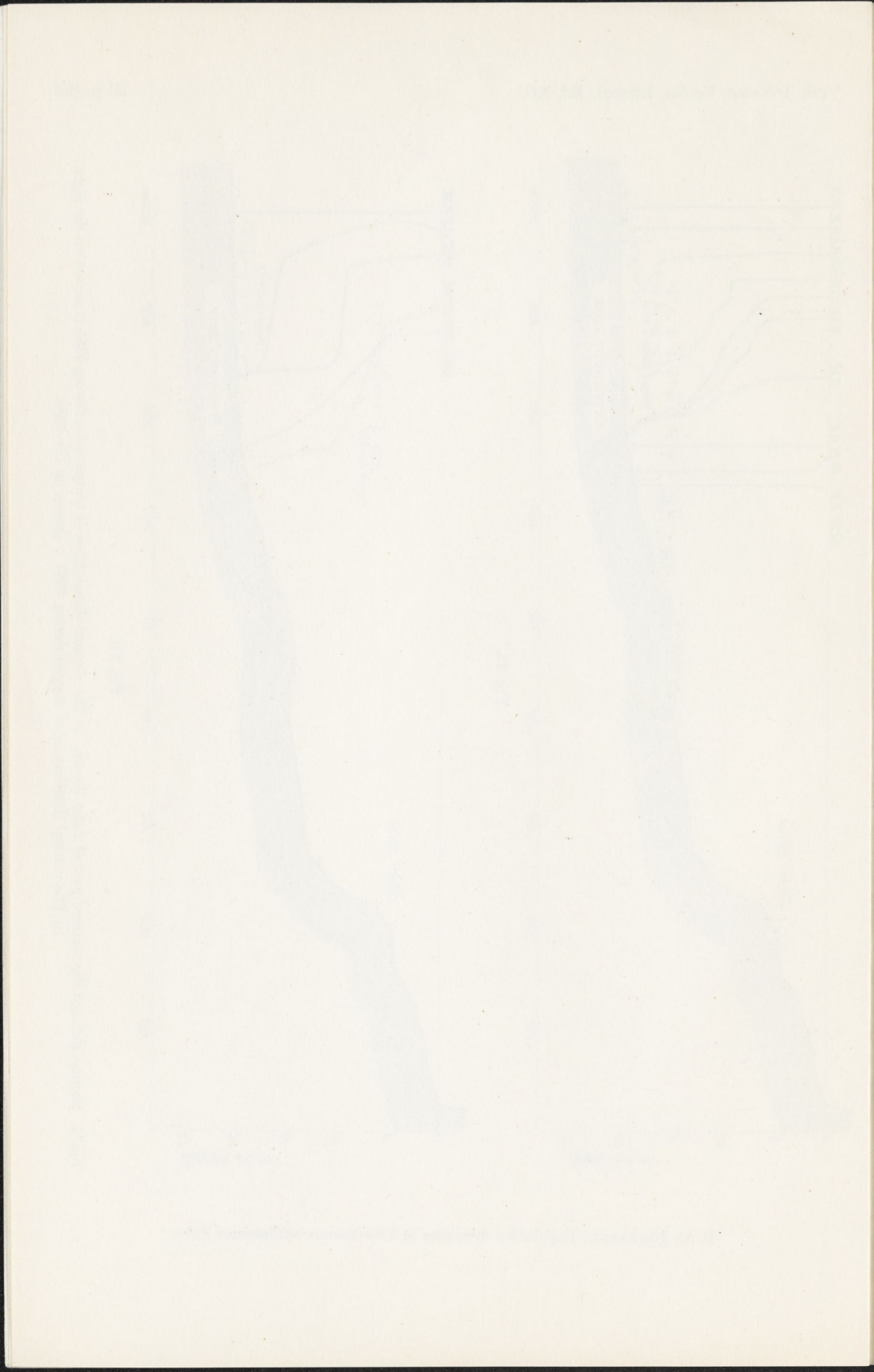


Fig. 2 b.

Fig. 2. Section through the western part of Lake Esrom. a) The vertical distribution of temperature during 1955 is shown on the right. b) The vertical distribution of oxygen during 1955 is shown on the right.



Ostracoda		<i>Candona candida</i> (O. F. MÜLLER) — VÁVRA <i>Candona neglecta</i> SARS <i>Candona protzi</i> HARTWIG
Copepoda	Cyclopidae Harpacticidae	<i>Cyclops viridis</i> JURINE <i>Canthocamptus</i> sp.
Diptera	Corethridae Chironomidae Chironominae	<i>Chaoborus (Corethra) flavicans</i> MEIGEN <i>Chironomus anthracinus</i> ZETT. (syn. <i>bathophilus</i> KIEFF., <i>liebeli</i> KIEFF.) <i>Procladius pectinatus</i> K.
	Tanypodinae	
Mollusca		<i>Pisidium henslowianum</i> SHEPPARD <i>Pisidium cinereum</i> ALDER <i>Pisidium lilljeborgi</i> CLESSIN

This community consists of specialists so far as feeding mechanisms and metabolism are concerned. *Chironomus anthracinus* and the tubificids are able to

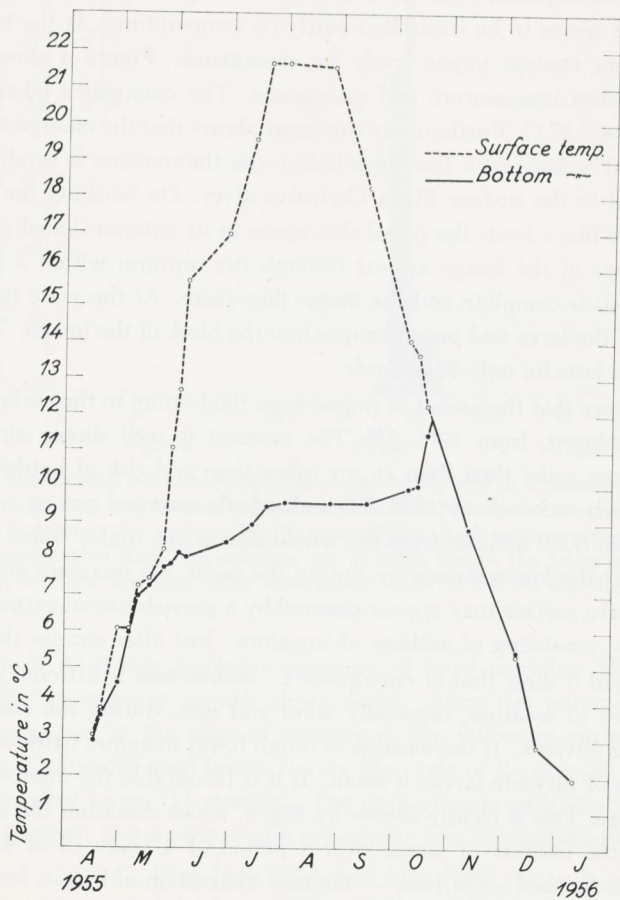


Fig. 3. Surface and bottom (18.5—19.0 m) temperature in Lake Esrom during 1955.

utilize oxygen at very low tensions because their blood contains haemoglobin. A physiological explanation of the presence of *Pisidium* in this biotope has not yet been found. *Corethra flavicans* migrates between the bottom, where it lives during the day, and the pelagic water layers, where it spends the night hours. Tanypodinae larvae only occur in the profundal zone during autumn, winter and spring, when the bottom layers are rich in oxygen.

The biology of *Chironomus anthracinus* ZETT.

The most important species according to numbers and weight in the above-mentioned community is *Chironomus anthracinus*.

This species swarms in thousands of millions at the same time as the leafing of the beeches takes place at the shore. This coincidence is of great importance since the beeches provide the necessary shelter for swarm formation along the coast.

The larvae inhabit the mud bottom, where they live in vertical tubes lined with silk. The metamorphosis from larva to pupa takes place gradually over a longer period, and it seems to be controlled partly by temperature. At the beginning of May the tubes contain pupae ready for emergence. Figure 4 shows the relationship between temperature and emergence. The emergence takes place at a temperature of 7,2° C. Furthermore the figure shows that the emergence is limited to 3 days and is finished a few days before the thermocline is established. The pupae ascend to the surface like a Cartesian diver. On reaching the surface the pupa behaves like a boat: the pupal skin opens in its anterior dorsal part, and the 1st pair of legs of the imago appear through the rupture; within a few seconds metamorphosis is complete and the imago flies away. At the same time the dark red colour of the larva and pupa changes into the black of the imago. This complicated process lasts for only 35 seconds.

Fig. 5 shows that the ascent of pupae from the bottom to the surface is limited to the night hours, from 19⁰⁰—1⁰⁰. The moment is well chosen since the lake is usually more quiet then than at any other time and risk of hatching failure is therefore much reduced. In 1956 500 individuals emerged per sq. m. per night, which is about 5000 millions from the whole lake in one night. Since the hatching takes place at the low temperature during the night, the imagines are not able to fly and the lake surface may appear covered by a greyish brown carpet (the colour of the wings) consisting of millions of imagines. Just after sunrise they fly away.

Figs. 4 and 5 show that at emergence *C. anthracinus* is extremely vulnerable. The influence of weather, especially wind and rain, during the short period of emergence is obvious. If the weather is rough fewer imagines hatch and the resultant number of juvenile larvae is small. If it is favourable the number of juvenile larvae is large. This is clearly shown by Fig. 6, which describes the seasonal fluctuations in the number of larvae over a period of 4 years. 3 or 4 weeks after emergence is finished — in June — the new generation of larvae, less than 2 mm long, is found in the mud layer. Growth is rapid during first weeks and the larvae

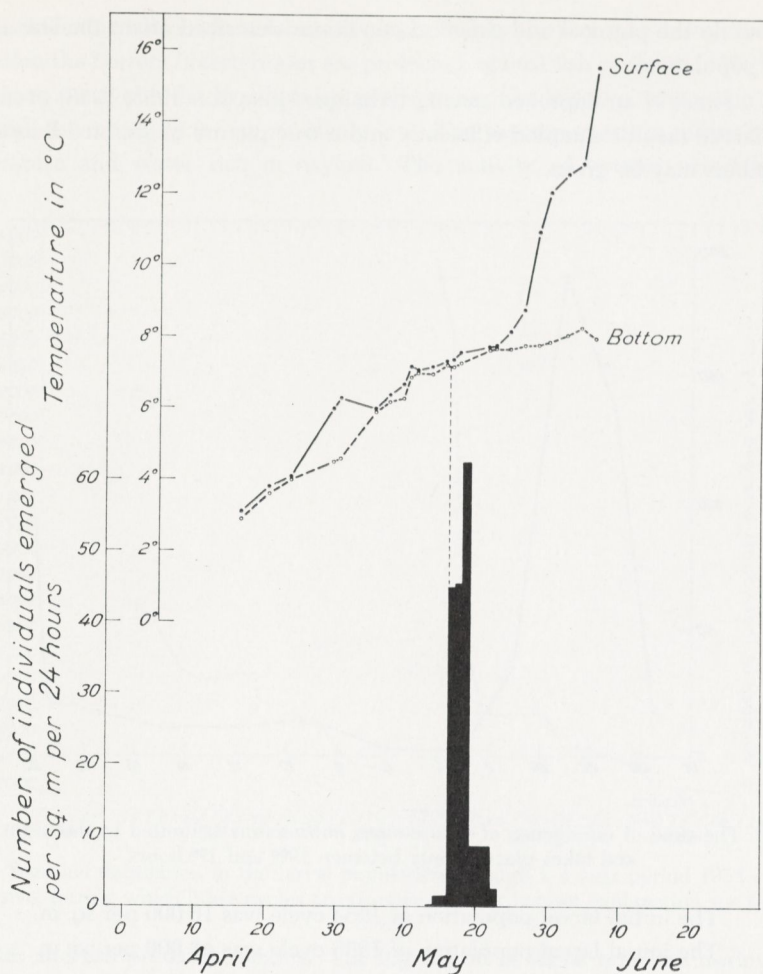


Fig. 4. The relationship between temperature and emergence in *Chironomus anthracinus* ZETT. Above: Surface and bottom temperature, below: Number of imagines captured in funnel traps just below the surface (cf. JÓNASSON 1954). Each column represents one day. Where, on consecutive days, the columns are of same height the traps have only been tended once, viz. the last day. The emergence starts at 7,2° C and lasts for 3 (—4) days only.

reach a size of 4—6 mm (compare diameter of head capsules, JÓNASSON 1955, Fig. 2). Later in summer growth slows down. After the autumn overturn it increases again and at the time of emergence the following spring the size is 16—18 mm. Ordinarily most larvae have a life cycle of 2 years (23 months), but some emerge after 1 year (11 months). The proportion in each group differs from one year to another. During the period in question two life cycles were completed:

from June 1954 until May 1956

from June 1956 until May 1958

How do the physical and chemical conditions described affect the size of the larval population?

As a result of an improved sieving technique (JÓNASSON 1955, 1958) even very small larvae may be sampled efficiently and a true picture of seasonal fluctuation in numbers may be given.

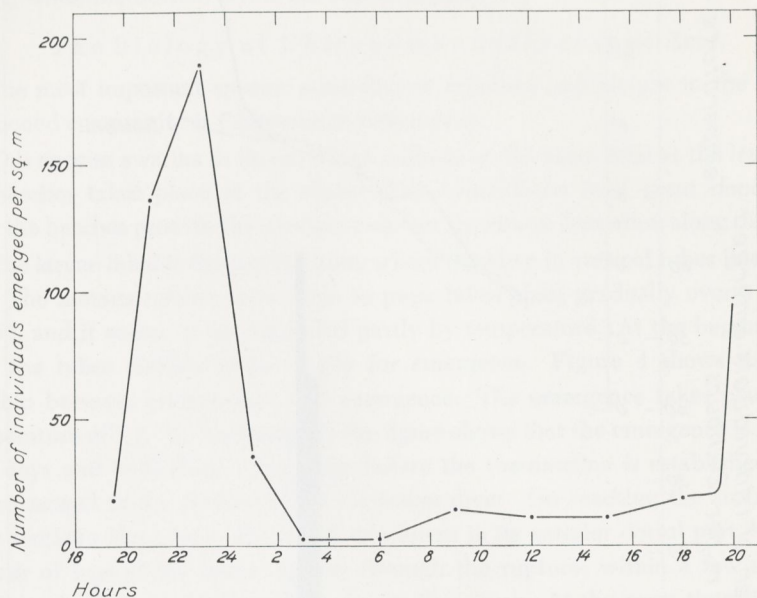


Fig. 5. The time of emergence of *Chironomus anthracinus* is limited to the night hours and takes place mainly between 19⁰⁰ and 1⁰⁰ hours.

The initial larval population of 1954 cycle was 16 000 per sq. m.

The initial larval population of 1956 cycle was 42 000 per sq. m.

The difference clearly shows that the initial numbers are highly dependent on weather conditions during the emergence period. Due to extremely favourable weather during the swarming period in May 1956 the new larval population reaches the above mentioned size of 42 000 individuals.

Mortality during the summer stagnation period is comparatively low:

In July—Sept. 1954 the larval population was reduced by 1500 per sq. m.

In July—Sept. 1956 the larval population was reduced by 5500 per sq. m.

while after the autumn overturn:

In Sept.—Nov. 1954 the larval population was reduced by 3 500 per sq. m.

In Sept.—Nov. 1956 the larval population was reduced by 24 000 per sq. m.

During winter the number of larvae is relatively constant. The sudden drop in number in May each year indicates time and size of emergence determined by funnel traps and bottom samples.

The wide fluctuations in numbers are explained by the fact that during summer stagnation the bottom invertebrates are protected against fish predation. No fishes are able to survive in the hypolimnion in this period, hence no consumption takes place and the mortality is comparatively low. The autumn overturn means higher temperature and water rich in oxygen. The activity of bottom invertebrates

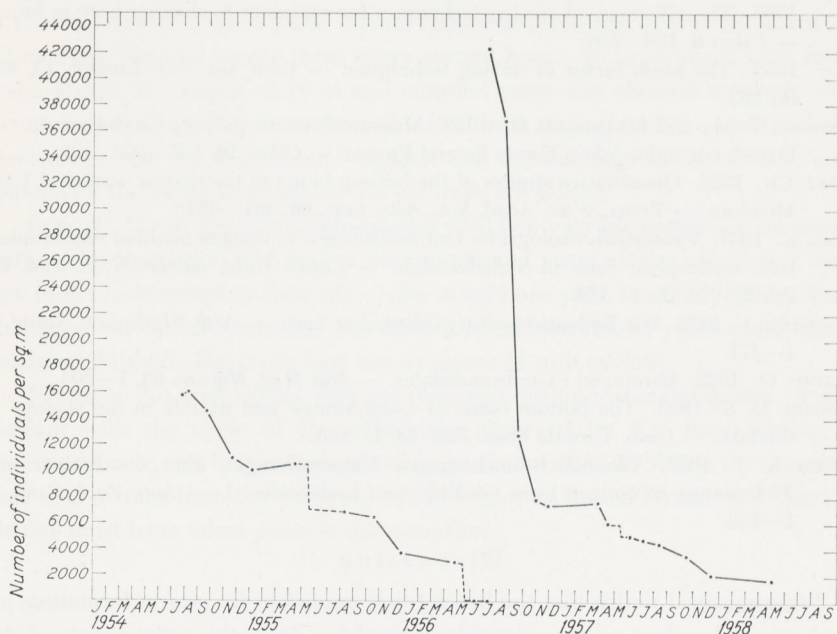


Fig. 6. Seasonal fluctuation in the larval population through a 4 year period 1954—1958 inclusive, during which 2 life cycles are completed. For further explanation see text.

increases and fish predation begins. The big fall off in larval numbers during the subsequent period is mainly due to consumption. During winter the activity of poikilothermic animals is low — e. g. the eels burrow into the mud — fish predation ceases and larval numbers remain constant.

In the profundal zone of Lake Esrom it is thus possible to consider separately mortality from fish predation and other forms of mortality in the population of *Chironomus anthracinus* at different seasons of the year.

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Discussion

REYNOLDSON: I notice that the beech trees, important for swarm formation, are much more abundant on the west side of the lake. Does this influence the distribution of the larvae in the lake?

JÓNASSON: The beech forest on the west side of the lake is of vital importance as shelter for swarm formation since the prevailing wind direction is south, south-west and west, and *C. anthracinus* swarms only in dead calm. Therefore the bulk of the egg masses may be expected to be deposited on the western lake shore. The south and south-western winds move the egg masses to the north and north-eastern part of the lake. This fact becomes clear from the initial numbers of young larvae of the 1956 generation. These numbers increase from south to north in the lake as follows (Fig. 1):

at st. I	38,184 individuals per sq. m.
at st. II	42,360 individuals per sq. m.
at st. III	56,072 individuals per sq. m.
at st. IV	70,920 individuals per sq. m.

MANN, K. H.: I noticed that there is a sharp rise in bottom temperature at the autumn overturn. Is this reflected in the life history of the animals?

JÓNASSON: After the autumn overturn the temperature may rise to 12—14° C and the water is rich in oxygen. This period of the year thus offers the most

favourable living conditions for the profundal invertebrate fauna. The oxygen uptake of *C. anthracinus* larvae increased up to 3 times and the average weight about 10 times in the first 3 weeks after the autumn overturn 1958.

BUSCEMI: Would you expect a difference in the diurnal emergence curve to occur if the emergence traps had been placed on the bottom sediments?

JÓNASSON: Not in the case of *C. anthracinus*. The practical difficulties are that it takes too much time to place several funnel traps on the bottom sediment in a 22 m deep lake and empty them every second hour. An experiment with funnel traps placed at a depth of 19 m and emptied every day showed numbers which do not materially deviate from those obtained from traps placed 3—4 metres below the surface. On the other hand I suggest that the numbers of *Corethra* obtained depend on the depth at which the funnel traps are placed.

BERG, C. O.: In discussing chironomids with two-year life cycles you mentioned only cycles that begin and end in even-numbered years. Since you stated that a few individuals complete their life-cycles in only one year, it would seem probable that two-year cycles beginning and ending in odd-numbered years could also be easily established. Have you seen any evidence of such cycles?

JÓNASSON: No, such cycles were not observed during this investigation. A comparison with the cycle of *C. anthracinus* observed by KAJ BERG during his investigation on the bottom animals of Lake Esrom 1932-34 shows the surprising fact that at that time the two-year cycles began in the odd-numbered years. A change must have taken place in the meantime.

Metabolism of an eutrophic reservoir¹

(Western Illinois University, USA)

JOHN DAVID PARSONS and ROBERT S. CAMPBELL (University of Missouri, USA)

With 2 tables in the text

Introduction

"The specific bioactivity of a biosystem is its capacity for the formation of potential energy and the subsequent reconversion of this into kinetic energy per unit of time and per unit of volume or surface area." (OHLE 1956.)

Thus, clearly and concisely, OHLE has outlined an approach to the classification of lentic bodies of freshwater by not narrowly defining the sum of both the productive and destructive processes carried on within such a body of water.

Reservoirs may be placed roughly in two categories: 1) those in which the exchange of water is so great as to be classified as modified lotic habitats and 2) those in which the exchange of water is rather small so as to be classified as relatively stable lentic habitats. There are hundreds of this latter type of reservoir in the midwestern United States which function as domestic water supplies and/or recreational areas.

Description of Area

Macrohabitat

The term "biosystem" as used in this study will encompass the watershed as well as the water mass or lake. The area of the biosystem amounts to 2,367 acres (959 hectares).

The biosystem is located near the 39th parallel 92nd meridian in the state of Missouri. Stream drainage is in a north-south direction to the Missouri River. Annual mean rainfall amounts to 35 inches (88.8 cm) in this oak-hickory plant association of the temperate deciduous forest formation.

Microhabitat

The area of the watershed is 2,345 acres (952 hectares), much of which is under cultivation. As a result, during periods of heavy rainfall the lake is quite turbid with a Secchi disc reading of 7 inches (17 cm).

¹ Contribution from the Missouri Cooperative Wildlife Research Unit: U. S. Fish and Wildlife Service, Wildlife Management Institute, Missouri Conservation Commission, Edward K. Love Foundation and University of Missouri cooperating.

The water mass, Ashland Lake, was formed in 1937 by impounding a narrow valley of Burlington limestone. The reservoir has an area of 17 acres (6.9 hectares) with a maximum depth of 32 feet (10 meters).

For ease in the interpretation of the data, the water mass was divided into two zones. This was deemed necessary on the basis of the per cent water-holding capacity loss which limited Zone 2 to the area of trophogenesis. Table 1 lists the physical data of the lake and of zones 1 and 2.

Table 1. Physical Data.

Areas	Surface area	Volume	Mean depth
Lake	$6.9 \times 10^4 \text{m}^2$	$18 \times 10^4 \text{m}^3$	2.7 m
Zone 1	$3.0 \times 10^4 \text{m}^2$	$17.2 \times 10^4 \text{m}^3$	5.7 m
Zone 2	$3.9 \times 10^4 \text{m}^2$	$0.8 \times 10^4 \text{m}^3$	0.2 m

Methods and materials

Bimonthly collections were taken of both physical and chemical data during the period August, 1952, through August, 1953, from Zone 1. Monthly collections of data were taken from Zone 2. Water temperatures were taken in both zones at one-foot intervals with a Foxboro thermophone.

From Zone 1 during the period of thermal stratification water samples were taken at the top and bottom of the epilimnion and at the top, middle and bottom of the hypolimnion, while spring, winter and fall samples were taken at the surface, 10, 20, and 30 feet. From Zone 2 monthly water samples were taken at the surface and bottom.

The chemical methods employed in the determination of ions for this study follow: dissolved oxygen, pH, and alkalinity by standard methods [carbon dioxide was calculated from the relationship between pH and the fractional activities of alkalinity and acidity constituents (MOORE 1939)]; soluble phosphate phosphorus and organic phosphorus by the ceruleomolybdic method, and ammonia nitrogen by direct nesslerization (ELLIS, WESTFALL AND ELLIS 1946); nitrite nitrogen by the alpha-naphthylamine acetate and sulfanilic acid method [the determination of low concentrations was facilitated by the normal-butyl alcohol modification (ZELLER 1955)]; and nitrate nitrogen by the phenoldisulfonic acid method (THEROUX et al 1936). The intensity of the color products of the colorimetric methods was determined by using a Hellige-Diller photoelectric colorimeter model 400.

Results

Net Primary Production

The conditions under which the carbon dioxide accumulation-oxygen deficit method of estimating net primary production (OHLE 1952) were applied and the calculated net primary production are listed in Table 2.

Table 2. Net Primary Production, Zone 1.

Method	Type of oxidation	No. of months	Gm C/m ² /mo
CO ₂ and O ₂	Aerobic and anaerobic	4	38.7
CO ₂	Anaerobic ^a	3	39.4
CO ₂	Anaerobic ^b	2.5	41.5
Nitrogen uptake	N/NH ₃ NO ₂ NO ₃	4	40.1
Phosphorus uptake	P/PO ₄	4	41.3
Biomass	P/organic	4	39.8

^a Thermal stratification not complete.

^b Thermal stratification complete.

On the basis that net primary production is primarily the formation of new protoplasm, and using the relationship 106 C : 16 N : 1 P (SVERDRUP et al 1942, and CLARKE 1948), net primary production was estimated from inorganic phosphorus uptake, inorganic nitrogen uptake (NH₃, NO₂ and NO₃), and organic phosphorus, as a measure of biomass (Table 2).

Considering all of the methods used, the calculated mean net primary production was 40.1 gm C/m²/mo [(39.8 gm C/m²/mo mean of carbon dioxide accumulation-oxygen deficit method) (40.4 gm C/m²/mo mean of nutrient uptake and biomass method)].

OHLE's method could not be used in the calculation of net primary production for Zone 2, which did not stratify. Inorganic phosphorus uptake, inorganic nitrogen uptake, and organic phosphorus, as a measure of biomass, methods were used. Net primary production per unit volume for both Zone 1 and Zone 2 was approximately the same; however, per square meter of surface area, Zone 2 produced only one-fifteenth as much as Zone 1 (2.66 gm C/m²/mo).

Energy Transfer

The method for estimating the amount of potential energy which becomes sedimentary, as given by OHLE (1956), was used to calculate the % utilization of potential energy. The utilization of potential energy in Zone 1 was calculated to be 82.5% (33.1 gm C/m²/mo).

However, when As/V becomes as great or greater than 1, i. e., $Dm = 1$ m or less, the method can no longer be applied, for mathematically $Cs = Cp$. As the mean depth of Zone 2 was 0.2 meter, no measure of the utilization of potential energy could be obtained by this method.

Bioactivity

The summation of the constructive and destructive processes of Zone 1 was 40.1 gm Cp plus 33.1 gm Cu or 73.2 gm C/m²/mo. Since it is not possible to determine the utilization of the potential energy for Zone 2 by the above method, no estimate of the bioactivity of this zone can be given.

Discussion

The laboratory work and lake investigations of OHLE (1956) indicate that the error which arises from carbon dioxide release from older sediments of lake origin is slight, and quite possibly such a positive error largely balanced the negative error resulting from the exchange of water masses across the metalimnion. However, the question arises as to the role played by allochthonous material in the evaluation of carbon dioxide accumulation as net primary production of eutrophic lakes. The major organic contribution from the watershed and from the higher aquatic plants enters the water mass of these lakes following the breakdown of thermal stratification.

In this study the oxidation of organic material during the period of winter stratification amounted to 43.6 gm C/m²/mo, less than one-half of which could be attributed to the water mass. This was based on photosynthetic rates given by VERDUIN (1956). The oxidation of this allochthonous organic material was complete, or nearly so, before the spring "bloom" of phytoplankton; thus, the accumulation of carbon dioxide during summer stratification could be attributed to the net primary production of the water mass. This conclusion was based on the following data: 1) the inorganic release of nitrogen and phosphorus, which reached a maximum in February, and the maintenance of this maximum following winter stagnation to the onset of the spring "bloom" of phytoplankton in April; 2) the maximum oxygen concentration and the minimum bicarbonate ion and carbon dioxide concentrations in March (between winter stagnation and the spring "bloom" of phytoplankton); and 3) a mean net primary production of 39.4 gm C/m²/mo the previous summer [carbon dioxide accumulation (anaerobic) and organic phosphorus as biomass].

It appears that OHLE's method of calculating net primary production can be profitably used for reservoirs under the following conditions: 1) if the outflow of water from the reservoir is restricted to the epilimnion, and 2) if winter oxidation is sufficient to break down all but the more reduced carbohydrates, i. e., the cellulose compounds.

However, the methods used did not determine total net primary production, but effective net primary production, i. e., the biomass that remained in the reservoir. The effective net primary production of this eutrophic reservoir was no greater than the net primary production of the northern German lakes studied by OHLE (1956). This was probably due to the loss of biomass with outflowing epilimnic water from the reservoir.

On the basis of effective net primary production this reservoir would be classified as an oligotrophic lake. To use bioactivity as proposed by OHLE (1958) would not change the classification as proposed by OHLE (1955).

It is suggested that reservoirs, and perhaps lakes, be classified on the basis of bioactivity per year, i. e., gm C/m²/year, as more carbon was released during the winter than was fixed during the summer in the reservoir studied. That this

approach is applicable to other reservoirs of this type was suggested by the fact that early spring zooplankton population maxima follow the release of organic fragments and occur before the spring "bloom" of phytoplankton. The occurrence of early spring zooplankton population maxima preceding the phytoplankton "bloom" has been observed in other reservoirs (PARSONS, unpublished data), implying the utilization of particulate organic material and/or organic molecular fragments by zooplankters. This further illustrates the influence of the energy contribution from the watershed and emphasizes the importance of estimating the bioactivity per year.

Summary

1. The effective net primary production, i. e., the biomass that remained in the water mass, was determined for an eutrophic reservoir (40.1 gm C/m²/mo).

2. The utilization of potential carbon amounted to 82.5% (33.1 gm C/m²/mo), and the bioactivity amounted to 73.2 gm C/m²/mo.

3. The carbon dioxide accumulation-oxygen deficit method can be profitably used to estimate net primary production in eutrophic reservoirs if 1) the outflow of water is restricted to the epilimnion, and 2) the amount of oxidation during the winter is sufficient to break down all but the more reduced carbohydrates.

4. On the basis of the carbon released during the winter and the loss of biomass with the outflow of epilimnic water, it is suggested that reservoirs, and possibly lakes, be classified on the basis of bioactivity per year, i. e., gm /m²/year.

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Discussion

HAYES: Do you assume the spring phosphorus maximum was from the sediment, following winter stagnation, or by inflow from the surrounding watershed?

PARSONS: It is felt that both the organic and the inorganic phosphorus maxima were due to the oxidation of allochthonous material which entered the lake during the fall turnover.

FISHERIES

SOME ESTIMATES OF PRIMARY PRODUCTION RATES IN MICHIGAN PONDS¹

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PHOTOSYNTHETIC fixation of solar energy in ponds is carried on by the attached algae (periphyton), by the planktonic algae, and by the larger plants growing on the pond bottom (aquatic macrophytes). In the present study we have attempted to: (1) measure independently rates of energy fixation by these three sources; (2) identify environmental factors which favor one source of production over the others; and (3) compare our production estimates with those made in other ecosystems.

It has been demonstrated experimentally that growth of aquatic macrophytes in some way inhibits phytoplankton production (Hasler and Jones, 1949). The mechanism of this inhibition remains obscure. Undoubtedly a variety of factors are involved and the degree of inhibition differs from one ecosystem to another. It has frequently been suggested that aquatic macrophytes compete with plankton algae for nutrient materials (Embrey, 1928; Bennett, 1942; Wiebe, 1934). However, shading effects (competition for light) have also been mentioned as mechanisms by which the larger aquatic plants suppress plankton blooms (Hasler and Jones, 1949). The position of periphyton algae in such competitive interaction has not been considered.

The chief methods of evaluating pond production have been measurements of the crops produced, such as bottom fauna and fish (Patriarche and Ball, 1949; Meehan, 1936; Hayne and Ball, 1956). In some instances, an index of the size of the plankton crop has been secured by making plankton counts and transparency measurements. Radioactive carbon (C^{14}) has been used to measure primary pro-

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duction in the ocean and in fresh-water lakes (Strickland, 1960). It affords a convenient and reproducible method of measuring production rates in ponds and should find useful application in pond culture, particularly in situations where one wishes to compare the production of one pond with that of another.

The attached algae have long been recognized as making a major contribution to the primary production of standing water (Young, 1945). However, few attempts have been made to estimate the energy fixed by this segment of the biota. Newcombe (1950) made quantitative measurements of the periphyton that accumulated on glass slides which were suspended in two southern Michigan lakes. His periphyton results tended to confirm his conclusions, based upon plankton and organic matter measurements, that Walnut Lake was more productive than Sodon Lake. Grzenda (1960) and Grzenda and Brehmer (1960) perfected quantitative techniques for studying periphyton. Grzenda showed that the phytopigments extracted from artificial substrates can be used to estimate the production of organic matter. It is appropriate that the C^{14} method and quantitative periphyton techniques be used to attack the general problem of the interrelationship between the production rates of periphyton, phytoplankton, and aquatic macrophytes.

METHODS AND MATERIALS

The information presented was collected at the Michigan State University experimental farm, Lake City, Michigan between June 15 and September 15, 1960. Routine chemical and physical measurements were made throughout this period. A continuous record of water temperature for the period was obtained from a Taylor thermograph. Hydrogen-ion concentration was determined with a Beckman pH meter (model H). Total alkalinity was measured by titrating samples with 0.02 N H_2SO_4 , using methyl-orange as an indicator (Ellis, Westfall, and Ellis, 1948). Dissolved oxygen was determined by the unmodified Winkler method. Total phosphorus was measured throughout the summer, using a modification of the procedure given by Ellis, Westfall, and Ellis (1948). Total iron was determined, using the tripyridyl method (American Public Health Association et al., 1955).

The accrual of periphyton on plexiglass plates yields an estimate of net primary production (Grzenda and Brehmer, 1960). Peri-

phyton was scraped from plates with a glass microscope slide and the phytopigment was extracted with 95 per cent alcohol. The ash-free dry weight of each periphyton sample was determined by evaporating the solvent and igniting the oven-dry samples in a muffle furnace at 520° C. Samples were weighed before and after ignition on an analytical balance. An estimate of ash-free dry weight of organic matter was obtained by subtracting the weight of ash from the dry weight.

The second source of primary production studied was the aquatic macrophytes. Thirty randomly selected samples of vegetation were obtained from each pond. Each sample consisted of all the plants within a one square-foot plot. All parts of the plants including roots and rhizoids were collected. Samples were drained a constant period of time and then weighed. This weight was recorded as wet weight. The last ten samples collected in each pond were taken to the laboratory for determination of dry weight. They were placed in an oven, dried at 55° C., and weighed. This weight was recorded as dry weight.

The third source of primary production studied was that from planktonic algae. The C¹⁴ technique as described by Steeman Nielsen (1951, 1952) and the oxygen method were both used to measure this source but the latter technique was abandoned when it became clear that results were not reproducible. Water samples were collected in a plastic container. Samples were introduced into glass-stoppered pyrex bottles which were suspended in the ponds at the depth at which the sample was collected. A series of three bottles was suspended at each depth. Two of the bottles were of clear glass and the third bottle was opaque. Bottles were suspended in each pond at depths of 16 and 32 inches. Before the bottles were suspended, two microcuries of C¹⁴, in the form of sodium carbonate, were added with a hypodermic syringe to each bottle. Bottles were exposed for a period of 6 hours, which began shortly after 9:00 A.M. At termination of the 6-hour exposure bottles were removed from the pond and a 25 ml. subsample from each bottle was filtered through a type HA, millipore filter pad. The pad was allowed to dry and was then cemented to a planchet. The planchet and attached filter pad were then placed in radiological counting equipment and counts of radioactive carbon were obtained. These counts were converted to total assimilated carbon, using the formulae given by Steeman Nielsen (1952b).

Results were expressed as milligrams of carbon fixed per cubic meter per hour.

Chelated iron (NaFeEDTA) was introduced into ponds B and C on July 15. The theoretical concentration of chelated iron in ponds B and C, after complete mixing, was one part per million. Diammonium phosphate was added to ponds C and D at a rate of 20 pounds per acre. The theoretical concentration of phosphorus after this treatment was 0.48 mg./l. for pond C and 0.41 mg./l. for pond D. Fertilizer and chelate were applied with a hand-operated garden sprayer. These materials were spread as evenly as possible over the entire surface of the ponds.

Between June 16 and 18, the ponds were drained and were not refilled until June 24. This period, during which the ponds lay fallow, was long enough to desiccate and kill the aquatic macrophytes.

PHYSICAL AND CHEMICAL

The general trend of the water temperature followed the temperature of the atmosphere very closely. The water warmed slowly until July 12 when we recorded a maximum of 84° F. Thereafter the ponds cooled gradually until September 8, when a sharp decline in water temperature was observed.

During the study period methyl-orange alkalinity varied between 46 and 96 ppm. and pH varied from 8.1 to 9.8. A decreasing trend in alkalinity and increasing trend in pH was observed in all ponds. The mean hydrogen ion concentration for the entire period varied very little from pond to pond. Mean pH values were as follows: pond A—9.03; pond B—9.25; pond C—9.3; pond D—9.1.

The dissolved oxygen concentrations in the ponds ranged from a maximum of 14.97 mg./l. in pond B to a minimum of 8.04 mg./l. in pond D. The dissolved oxygen trend was quite similar in each pond. There was an initial period of low oxygen concentration followed by an increase to a maximum on August 1. Following this peak, oxygen values remained high but fluctuated considerably for the duration of the study.

INFLUENCE OF POND DRAINAGE ON CHEMICAL CONDITIONS

Draining the ponds prior to the study apparently had a pronounced influence upon the concentration of nutrients in the water.

It is well known that allowing ponds to dry and lie fallow releases nutrients from bottom soils (Mortimer and Hickling, 1954).

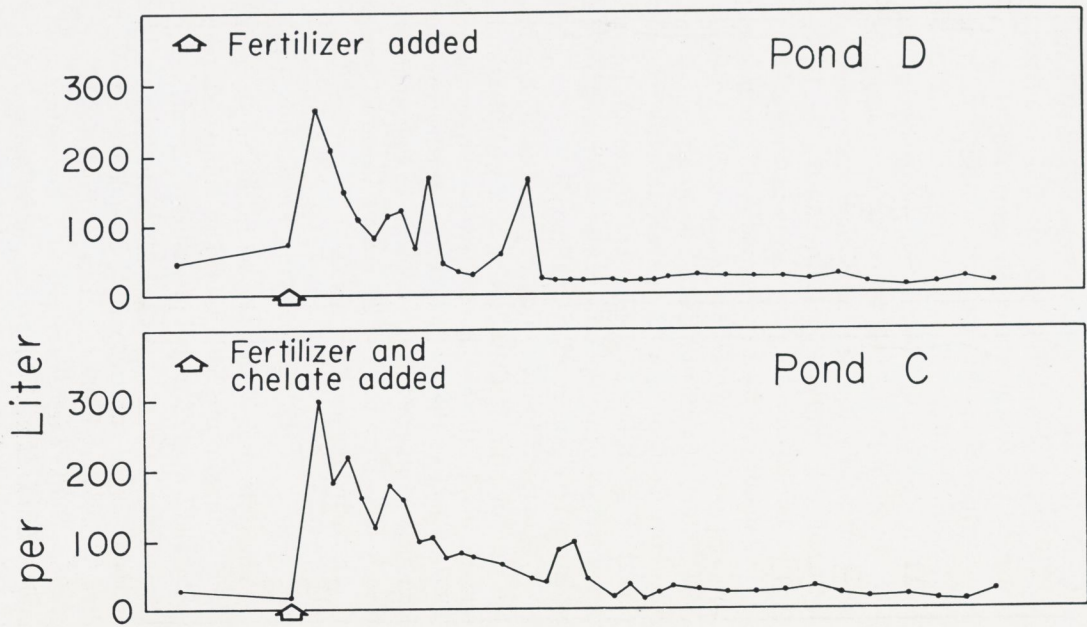
The total phosphorus concentration in all experimental ponds reached a peak on precisely the same date (Fig. 1), indicating that some factor was operating simultaneously in all ponds to bring phosphorus into solution. This peak might have been attributed to the addition of chelate and fertilizer in the ponds receiving this treatment were it not for the fact that the control pond not only exhibited this peak but nearly equaled the phosphorus concentration recorded in the ponds receiving artificial enrichment (Fig. 1). This peak in phosphorus concentration is almost certainly an effect produced by drying and disturbing the bottom mud and by release of phosphorus after decomposition of the bottom vegetation. An excess of phosphorus over the actual needs of the plankton algae and bottom vegetation may have been present for a short time at the onset of the study period (Fig. 1), but as the bottom vegetation began to flourish, the concentration of phosphorus in the water steadily diminished, until a plateau level was reached in all ponds.

A situation similar to that observed for phosphorus developed in the case of iron. With fallowing and with death and decay of the aquatic plants, there seems to have been return of iron to the water. Thus we believe that if there were any effects produced by the chelating agent and fertilizer upon iron and phosphorus concentrations, these effects were masked by large releases of iron and phosphorus that occurred upon reflooding.

PERIPHYTON PRODUCTION

The term periphyton as used in this paper is defined by Odum (1959): "organisms, both plant and animal, attached or clinging to stems and leaves of rooted plants or other surfaces projecting above the bottom." The composition of the periphyton biocoenosis living on the artificial substrates in the ponds was as follows: most abundant forms were representatives of the green algae, such as *Oedogonium*, *Bulbochaete*, *Scenedesmus*, *Tetraedron*, and *Oocystis*; desmids (*Cosmarium*, *Micrasterias*, and *Staurastrum*) were somewhat less abundant; diatoms, such as *Nitzschia*, *Fragilaria*, *Cymbella*, and *Diatoma* were encountered only occasionally.

Net production was measured in all ponds for the period from



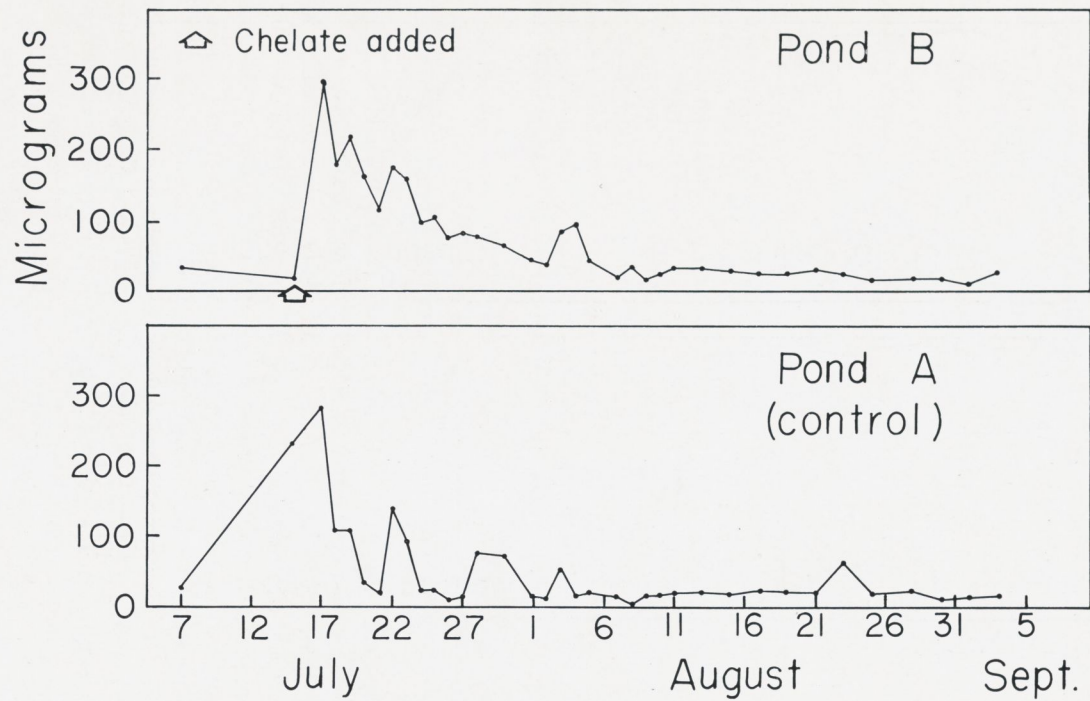


FIG. 1. Total phosphorus concentration in ponds in 1960.

TABLE I
NET PRIMARY PRODUCTION AS DETERMINED BY PERIPHYTON
ACCURAL ON ARTIFICIAL SUBSTRATA
(ash-free dry weight)

Collection Date (1960)	Exposure Period (days)	Net Production (grams per sq. meter per day)							
		Mean				Standard Deviation			
		Pond				Pond			
		A	B	C	D	A	B	C	D
7-5	12	0.212	0.190	0.278	0.301	0.032	0.016	0.043	0.028
7-14	9	0.298	0.259	0.290	0.331	0.000*	0.026	0.068	0.003
7-21	7	0.390	0.332	0.690	0.522	0.039	0.010	0.054	0.017
7-28	7	0.390	0.337	0.528	0.417	0.094	0.025	0.017	0.019
8-4	7	0.450	0.297	0.586	0.394	0.031	0.026	0.091	0.012
8-11	7	0.428	0.325	0.404	0.437	0.036	0.051	0.018	0.035
8-18	7	0.394	0.372	0.395	0.411	0.031	0.030	0.063	0.032
8-25	7	0.266	0.332	0.394	0.351	0.038	0.034	0.008	0.032
9-1	7	0.296	0.242	0.265	0.280	0.011	0.034	0.002	0.029
Mean		0.347	0.298	0.426	0.383				

* Single sample.

June 24 to September 1, 1960 (Tab. I). Each pond followed a slightly different week-to-week trend in accrual of organic weight, but a similar general trend was observed in all ponds. Low production in the latter part of June and the first part of July was followed by maximum production during midsummer and a decline in production in late August and early September. Mean net production rates for the summer were as follows: in pond A it was estimated to be 0.347 grams ash-free dry weight per square meter per day; in pond B, 0.298; in pond C, 0.426; and in pond D, 0.383 grams of ash-free dry weight per square meter per day. These values represent production during the summer, hence are probably much higher than a yearly average.

PRODUCTION BY AQUATIC MACROPHYTES

The principal macrophytes in the ponds, in order of their importance, are as follows: *Chara* sp., *Potamogeton pectinatus*, *P. zos-*

TABLE II
NET PRIMARY PRODUCTION OF POND MACROPHYTES DURING THE 1960 GROWING SEASON, AS DETERMINED BY THE HARVEST METHOD

Pond		Weight			
		Mean			Standard Deviation
		Pounds per acre	Grams per sq. meter per day	Grams per sq. meter	Grams per sq. meter
A	Wet	11,771		1,322	107
	Dry	1,047	1.45	118	42
B	Wet	38,533		4,326	330
	Dry	2,360	3.27	265	86
C	Wet	25,274		2,838	530
	Dry	2,042	2.83	229	181
D	Wet	22,272		2,501	331
	Dry	4,329	6.00	486	263

teriformis, *P. natans*, *Carex* sp., *Scirpus* sp., *Typha latifolia*, *Sagittaria* sp., *Elodea canadensis*, *Equisetum fluviatile*, *Eleocharis* sp., and *Najas flexilis*.

The mean net productivity value obtained for each pond is given in Table II. Values ranged from a high of 6.00 grams dry weight per square meter per day in pond D to a low of 1.45 grams dry weight per square meter per day in pond A.

PHYTOPLANKTON PRODUCTIVITY

The predominant planktonic forms were rotifers, desmids, and flagellates. Rotifers were represented by *Keratella* sp. and *Notholca* sp. Desmids were represented by *Cosmarium* sp., *Staurastrum* sp., and *Micrasterias* sp. Flagellates were represented by the dinoflagellate (*Ceratium hirundinella*, Stein), and three genera from the order Volvocales (*Eudorina* sp., *Pleodorina* sp., and *Volvox* sp.). Other forms frequently observed were copepods and cladocera. The copepods were chiefly *Macrocyclus* sp., whereas the cladocera were rep-

resented by *Bosmina* sp. Diatoms were rare in the pond plankton samples.

The radioactive carbon method used in the present study yields a measure of photosynthesis that is somewhere between the net and gross value, possibly nearer to the former (Strickland, 1960). These data are presented in tabular form in Table III. A maximum carbon assimilation value of 23.7 mg. of carbon per cubic meter per hour was recorded in pond D at the exposure depth of 16 inches on July 24, 1960. The minimum carbon assimilation value was 2.75 mg. of carbon per cubic meter per hour in pond A on July 10, 1960, at a depth of 32 inches.

COMPARISON OF PRODUCTION ESTIMATES

Production rates as measured by the methods outlined above show variations from pond to pond (Tab. IV). There is, however, a close agreement in the order of various ponds when they are ranked using the C^{14} method and using the dry weight of macrophytes. Both of these estimates suggest that pond A is least productive, followed by pond C. Pond B has a somewhat greater mean production than either pond A or C, but is considerably less productive than pond D. The four ponds cannot be ranked in the same order using the periphyton method of measuring primary production. The periphyton method indicates that the lowest production rate occurred in pond B and the highest in pond C. Ponds A and D were intermediate. An estimate of total accrual of periphyton in the ponds cannot be calculated without information on the average area of substrata suitable for colonization. Thus rates of accrual on artificial substrates are only indices of the intensity of this source of production. If the heavy growth of macrophytes in pond D provided the largest surface area for periphyton growth, then this pond might have had the highest total of periphyton production.

Table IV gives some estimates of primary production in other ecosystems as well as a summary of estimates for the ponds. Values for production in terms of carbon have been converted to organic matter using a factor of 2.0 (Ryther, 1946). Comparing phytoplankton production of the ponds with other ecosystems suggests that production is comparatively low in the ponds. The ponds compare favorably with primary production reported for some parts of the ocean and with values reported for an unproductive lake in Michi-

TABLE III
 PRIMARY PRODUCTION MEASUREMENT IN PONDS, USING THE C¹⁴ METHOD
 (Assimilated carbon is expressed as milligrams of carbon per cubic meter per hour.)

Exposure Date	Pond								Weather Conditions during Exposure	Water Temperature during Exposure (degrees F.)
	A		B		C		D			
	Depth (inches)		Depth (inches)		Depth (inches)		Depth (inches)			
	16*	32	16	32	16	32	16	32		
7-20-60	4.35	4.42	6.66	8.90	12.54	12.68	7.29	11.16	Very bright, clear	74
7-27-60	4.86	3.52	6.05	4.83	9.36	6.11	8.41	12.71	Clear, few clouds	78
8- 3-60	5.83	4.32	12.44	10.27	10.46	8.69	14.83	15.60	Partly cloudy	79
8-10-60	3.68	2.75	7.68	7.57	8.66	7.53	14.35	15.15	AM—overcast	73
8-17-60	7.87	6.82	10.17	9.15	8.36	9.59	15.76	22.60	PM—partly cloudy	
									AM—clear	74
8-24-60	4.89	4.36	7.72	7.76	9.30	6.90	23.75	22.70	PM—overcast	
									AM—clear	76
8-31-60	7.44	7.96	11.59	9.15	8.26	6.83	11.37	10.60	PM—overcast	
									Overcast to partly cloudy	78
9- 7-60	7.11	7.14	11.33	13.76	8.90	8.68	18.38	11.99	Slightly overcast	82
Mean value	5.75	5.17	9.21	8.92	9.48	8.38	14.27	15.31		
Mean of 16- and 32-inch depths	5.46		9.07		8.93		14.79			

One dark bottle and two light bottles were exposed for six hours at each depth.

* All exposure depths were measured from the surface of the pond to the sample.

TABLE IV
COMPARISON OF PRIMARY PRODUCTIVITY ESTIMATES FOR VARIOUS ECOSYSTEMS

Location	Method	Production Rate				Source
		Grams of organic matter per sq. meter per day		Macrophytes (Dry weight)		
		Phyto-plankton	Peri-phyton	Grams per sq. meter per day	Pounds per acre	
Pond A		0.30	0.35	1.45	1,047	
Pond B		0.48	0.30	3.27	2,360	
Pond C		0.44	0.44	2.83	2,042	
Pond D		0.64	0.38	6.00	4,328	
Blind Lake, Michigan		1.20				Schelske, 1960
Barents Sea	C ¹⁴	0.56				Corlett, 1957*
North Sea (annual range)	C ¹⁴	0.20-3.00				Steel, 1957*
South Atlantic	C ¹⁴	1.00-8.00				Steeman Nielsen, 1954
Red Cedar River, Michigan	Periphyton accrual		0.56			Grzenda, 1960
Silver Springs, Florida	Organic weight			7.40		H. T. Odum, 1957
Sargasso Sea	Organic weight	0.26				Riley, 1957
Seaweed beds, Nova Scotia	Harvest			1.00		Tamiya, 1957
Wheat (world average)	Harvest			2.30		Woytinsky and Woytinsky, 1953
Green Lake, Wisconsin	Harvest				1,590	Rickett, 1924
Lake Mendota, Wisconsin	Harvest				1,801	Rickett, 1922

* Quoted by Strickland, 1960.

gan (Blind Lake). Periphyton accrual rates are similar to those observed in a warm-water stream in southern Michigan (Tab. IV). Net production of larger plants in the most productive ponds was 2.4 times greater than that in Lake Mendota and 2.7 times greater than that in Green Lake (Tab. IV). Since these Wisconsin lakes are of high productivity it would seem that the level of production by aquatic macrophytes in the ponds is relatively high.

From the foregoing it would appear that production rates of phytoplankton in these ponds are low but that the rates of larger plants

are rather high. It is hypothesized that the comparatively low production rates of phytoplankton as compared to macrophytes can be explained in terms of adaptive mechanisms available to larger plants and absent in phytoplankton. The rate of photosynthesis by phytoplankton cells is strongly influenced by light intensity. It increases with increasing intensity until a saturation value is reached. Above the saturation value, the rate remains constant with increasing intensity up to a critical intensity at which it decreases due to light inhibition of the photosynthetic process (Strickland, 1960). Inhibition is brought about by photooxidation of critical enzyme systems (Steeman Nielsen, 1952c). At high intensities, there is a bleaching of the chlorophyll in algal cells.

In shallow, transparent ponds the light intensity at all depths is a large fraction of that at the surface. According to Oosting (1958), in the presence of intense light larger plants exhibit elongated palisade cells. Cutin is thicker and the amount of supporting tissue is greater in intense light. Oosting (*ibid.*) indicates that during intense illumination chloroplasts arrange themselves along the side walls of palisade cells and thus receive a minimum of direct insulation. The possession of mechanisms adapting aquatic macrophytes to intense light may have enabled them to grow in luxuriant beds, while the phytoplankton, without such mechanisms may have been light-inhibited. Flooding ponds in early summer when there is little cloudiness may favor growth of aquatic macrophytes as compared to phytoplankton whereas the lower light intensities of a cloudy spring may favor growth of phytoplankton.

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Effects of impoundment on water chemistry and plankton in Lake Ransaren (Swedish Lappland)

WILHELM RODHE (Uppsala, Sweden)

With 8 figures on 4 folders

Introduction

In recent years many lakes in northern Sweden have been — and others will be — impounded in order to provide continuous water supply to hydro-electric power plants further downstream. Their natural water-level is raised by means of a dam across the outlet, and in lakes used for annual storage the high level obtained during summer and autumn is followed by low water in late winter and early spring. These fluctuations cause a “dead”, eroded zone along the shore, the most depressing feature of impounded lakes.

Less obvious are the impoundment effects upon limnic metabolism and production. An initial increase of fish growth and fishing yield has sometimes been observed, but we still lack detailed studies of how the biota, the “food chains”, respond to the environmental changes. To ensure valid conclusions we need comparable data not only for a sufficiently long period following the first damming, but also for the original, undisturbed, conditions. The latter information is, in most cases, completely absent or very poor.

A long-term study of the particular lake alone does not suffice, however, for a safe interpretation of results. The properties of every lake are more or less submitted to variations from year to year because of climatic differences between the years. Thus it may be impossible to distinguish climatic effects from those actually caused by impoundment. To avoid, as far as possible, this source of error, the investigation has to include parallel observations from a “blank” lake, similar and adjacent to the impounded one but not disturbed by man.

Impoundment and investigation

In its course from the mountains at the Norwegian border to the Gulf of Bothnia, the river Ångermanälven drives several power stations. In the upper part of its drainage area, in southern Lappland (65° N, 15° E), the lakes Ransaren and Kultsjön are among the most important storage basins. They are situated at about 580 m and 540 m, respectively, above sea level and have the following dimensions:

	length km	area km ²	max. depth m
Ransaren	14	21	60
Kultsjön	30	53	140 (east basin)

Both lakes have outflows at the southern end (Fig. 1). After passing through a smaller lake (Gikasjön), the brook from Ransaren enters Kultsjön in the northern corner of its trisected basin. The main sampling station in Kultsjön has been in the western basin, which is divided from the other parts by a shallow constriction. It is, therefore, rarely influenced by water from Ransaren.

The dam construction across the outlet of Ransaren started in the winter 1953/54. In settling the terms for the impoundment of the lake, the Water Court prescribed a thorough and comprehensive investigation in order to gain better fundamental knowledge as to the effects of the impoundment upon fish production and the conditions for it, locally as well as generally.

The project was performed as team work: The Institute of Freshwater Research, Drottningholm (director Prof. S. RUNNSTRÖM), made the studies on fish biology and bottom fauna, while the Institute of Limnology, Uppsala, under my guidance took the general limnological aspects, in particular chemical conditions and plankton.

In the present paper, not more than a short review can be given of some essential results obtained by the Uppsala group.¹ A full account is available in mimeographed reports (in Swedish) and will also be published, as a number of papers, in the Reports of the Institute of Freshwater Research, Drottningholm (two zooplankton papers, by J. AXELSON, appeared in Report No 42, 1961).

At the beginning of the joint investigations, in June, 1954, it was decided to extend them to Kultsjön as well. The two lakes — typically oligotrophic from all points of view — appeared quite similar, and the results from the western basin of Kultsjön were expected to serve as a useful measure of undisturbed conditions. This proved to be true, until the construction of a dam across the outlet and the deforestation along the shores started also at Kultsjön, in 1958. From that year on, changes in Kultsjön may have been due partly to human action, interfering with climatic and other natural factors.

The Ransaren dam permits a regulation interval of 18 m: 12 m above and 6 m below the original mean level. Its full capacity was used for the first time in 1957, when the gate was almost closed from spring to late autumn. The water rose high above the former shore line, flooding meadows and previously wooded slopes. After the winter withdrawal, on the other hand, great littoral areas were exposed to air and erosion. Both changes of the level favour the transport of suspended and dissolved matter into the lake.

¹ L. KARLGREN and O. LINDGREN: Physical and chemical conditions. A. NAUWERCK: Phytoplankton. W. RODHE: Primary production. J. AXELSON: Zooplankton.

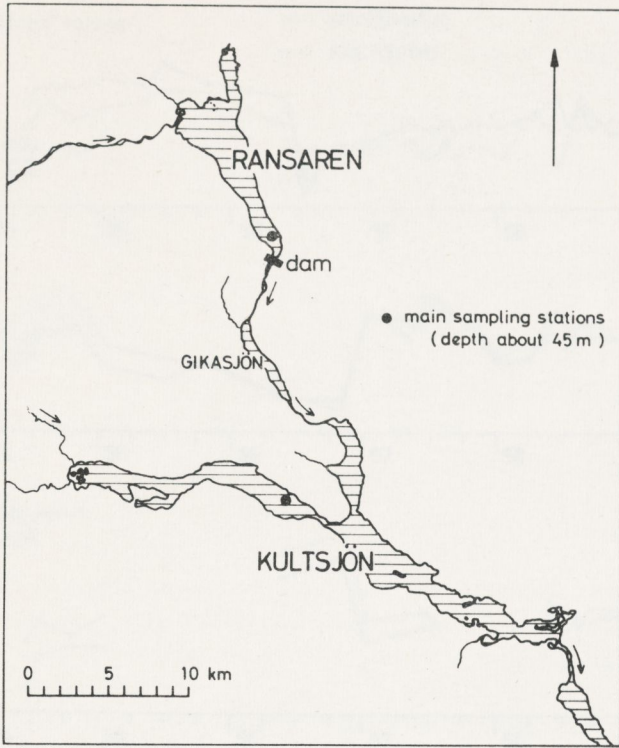


Fig. 1.

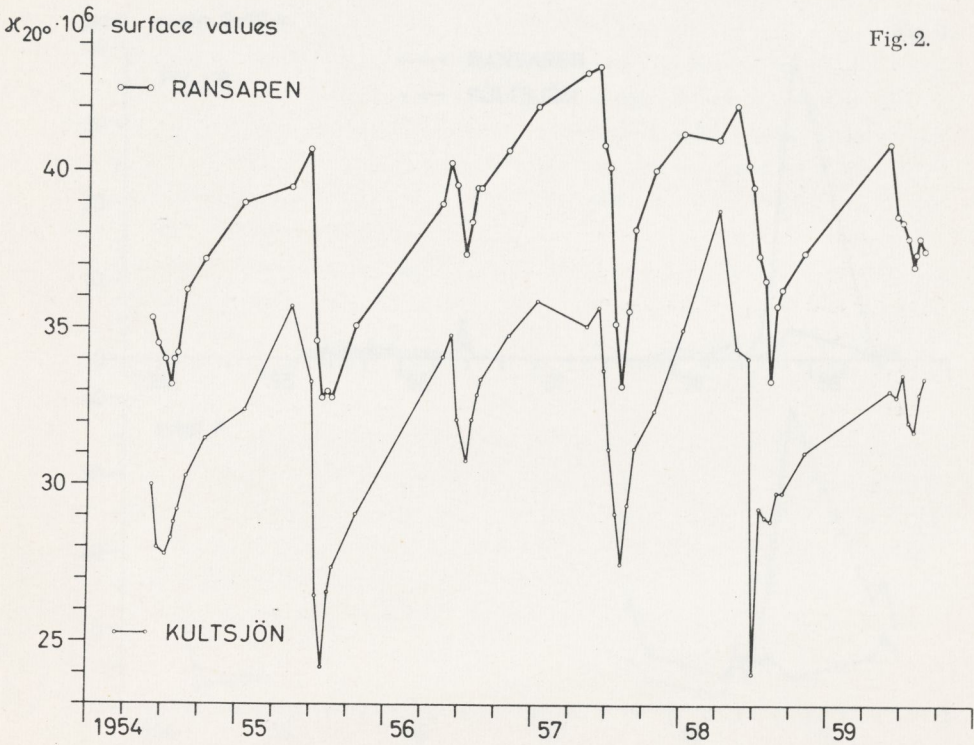
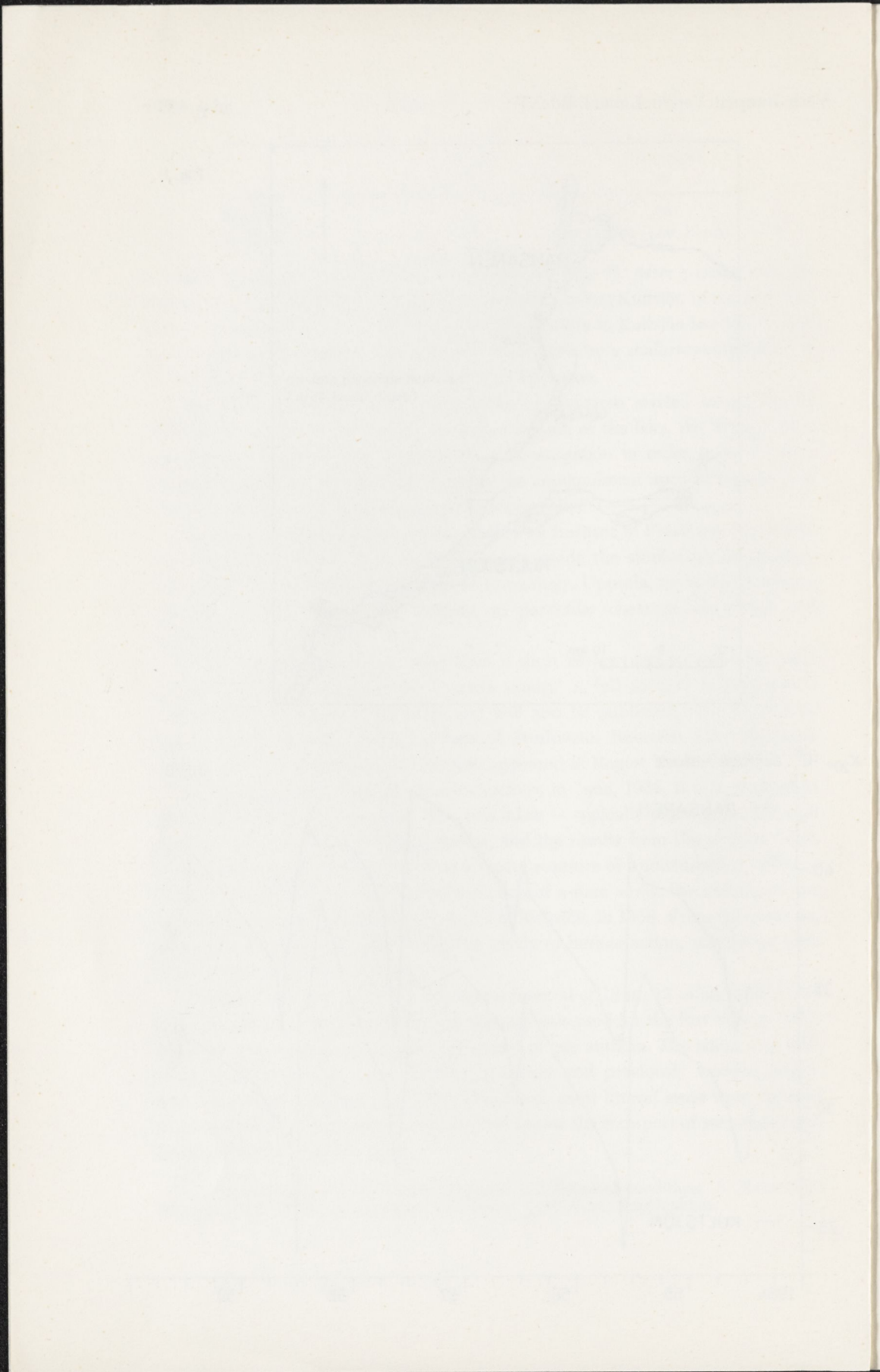
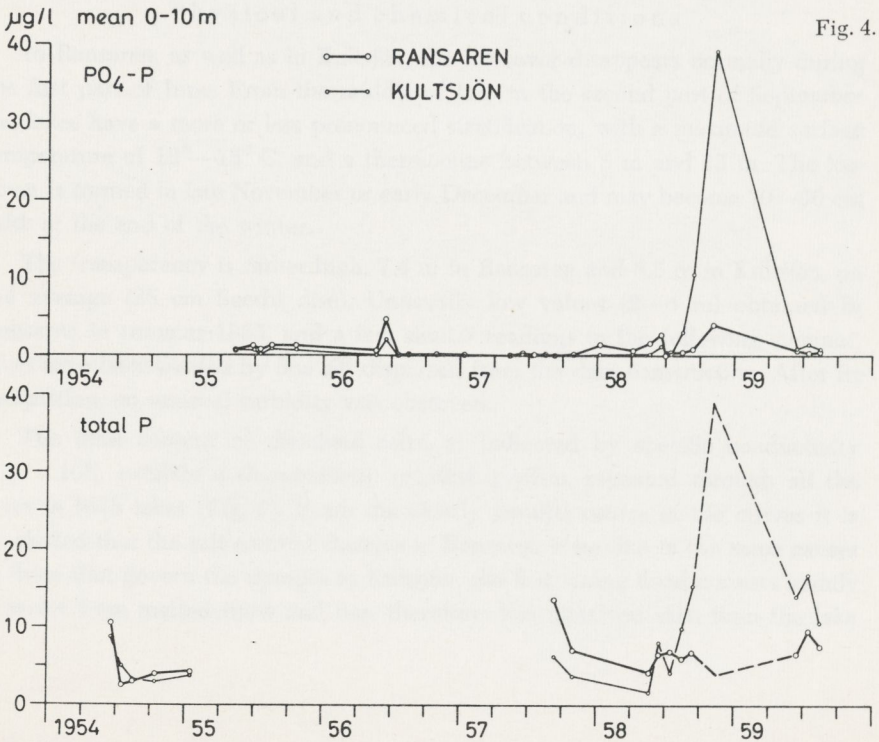
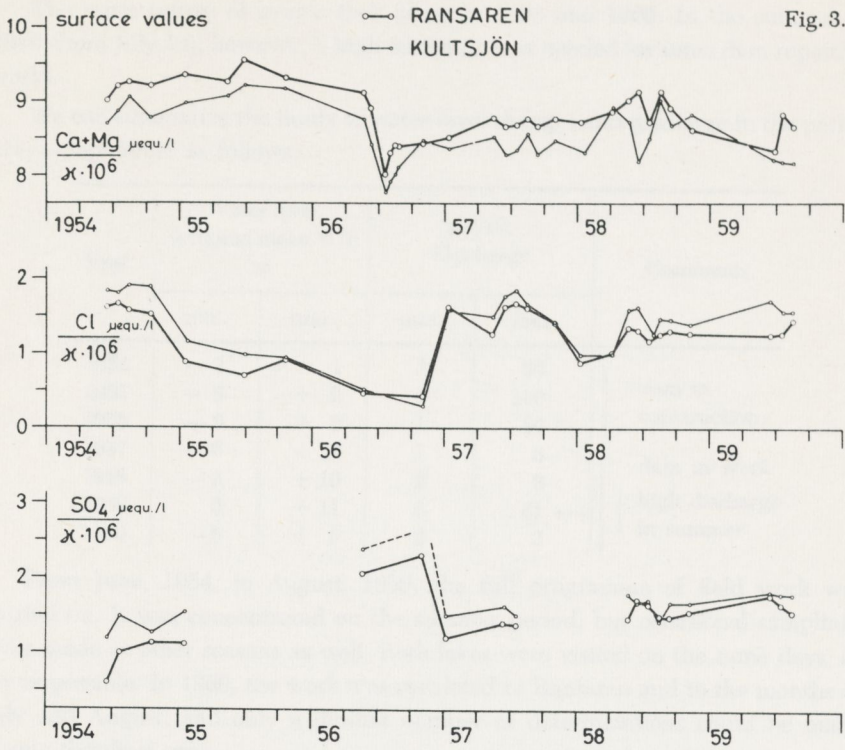


Fig. 2.







The same course of events took place in 1958 and 1960. In the summer of 1959 (from July 14), however, a high discharge was needed for some dam repairing works.

We can summarize the limits of water-level changes and discharge in the period May—September as follows:

Year	Water level (original mean = 0) m		m ³ /sec Discharge		Comments
	min.	max.	min.	max.	
1954	— 2	+ 1	3	90	} dam in construction
1955	— 6	+ 2	1	100	
1956	— 6	+ 2	1	80	
1957	— 6	+ 11	1	3	} dam in work
1958	— 2	+ 10	2	3	
1959	0	+ 11	2	41 ←	} high discharge in summer
1960	— 6	+ 9	2	3	

From June, 1954, to August, 1959, the full programme of field work was carried on. It was concentrated on the summer period, but occasional samplings were made at other seasons as well. Both lakes were visited on the same days, as far as possible. In 1960, the work was restricted to Ransaren and to the months of July and August, and only a limited number of determinations could be made during that final year.

Physical and chemical conditions

In Ransaren, as well as in Kultsjön, the ice-cover disappears normally during the first part of June. From the middle of July to the second part of September the lakes have a more or less pronounced stratification, with a maximum surface temperature of 12°—15° C, and a thermocline between 5 m and 15 m. The ice-cover is formed in late November or early December and may become 70—90 cm thick at the end of the winter.

The transparency is rather high, 7.4 m in Ransaren and 8.5 m in Kultsjön, on the average (25 cm Secchi disc). Unusually low values (2—4 m) obtained in Ransaren in summer 1955, and a few similar readings in the following summer, must have been caused by fine silt dispersed from the dam construction. After its completion, no unusual turbidity was observed.

The total content of dissolved salts, as indicated by specific conductivity ($\kappa_{20^{\circ}} \cdot 10^6$), exhibits a characteristic seasonal rhythm, repeated through all the years in both lakes (Fig. 2). From the closely parallel course of the curves it is concluded that the salt content changes in Ransaren were due to the same causes as those that govern the changes in Kultsjön: the first spring flood consists mainly of water from melted snow and has, therefore, less dissolved salts than the lake

water, but from July until winter the tributaries bring more salts to the lakes. Compared with these natural variations, the effect of the impoundment on the total salt content is negligible, if indeed there is any.

Whereas the total amount of electrolytes varies regularly during the year, the ionic composition seems to change more at random on a long-term trend (Fig. 3). In the first three years of the study, calcium and magnesium had a rather high, and chloride (and sodium) a low or decreasing, share in the total salt content (conductivity). In the following years the situation was about the opposite. The few data available for sulphate indicate that this ion showed trends opposite to those of chloride. If these changes had been known for Ransaren only, it would have been tempting to correlate them with the impoundment. The similar variations shown by Kultsjön reveal that there must have been other causes, such as variations from year to year in the atmospheric circulation, precipitation, and supply of cyclic (marine) salts.

The level of the phosphate content was slightly higher in Ransaren than in Kultsjön during 1955 and the first part of 1956, when the brush was cleared and burned on the shores. The same clearing was done at Kultsjön in summer and autumn 1958, and no other cause can be found for the large increase of phosphate in its upper layer at that time (Fig. 4). If we discard Kultsjön as "blank" control for phosphate in the latter half of 1958, we cannot be sure that the simultaneous phosphate increase in Ransaren was due to the impoundment. This appears very probable, however, since the higher values in Ransaren were noted even, and to a greater extent, in the first part of that year when Kultsjön still had an unchanged phosphate level. The curves for total phosphorus are too incomplete to permit a detailed discussion, but in 1958 and 1959 its level seems to have been higher than in 1954 for both lakes.

Nitrate (Fig. 5) shows about the same seasonal rhythm in both lakes, with maximum values in winter and early spring, and a minimum at summer. In contrast to phosphate, the nitrate level does not seem to have been significantly raised by the shore clearing or after the first impoundment. Total nitrogen, on the other hand, resembles total phosphorus in being higher, for both lakes, in 1958—59 than in 1954.

Phytoplankton and primary production

Quantitative variations of total phytoplankton are most reliably recorded by volume (Fig. 6). To begin with the "control" in Kultsjön, no trend can be seen from 1954 to 1959; apart from a peak in 1955, the mean level for the period June, July, and August was more or less unchanged.

In contrast to the "steady state" in Kultsjön, the phytoplankton in Ransaren increased definitely in 1958 (the year after the first full impoundment), and still more in 1959. The faint signs of an increase in 1956 and 1957, particularly for the autumnal standing crop, could be interpreted as effects of brush burning and

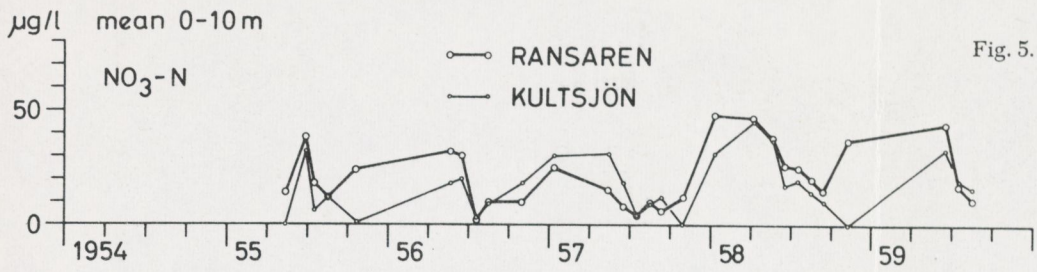


Fig. 5.

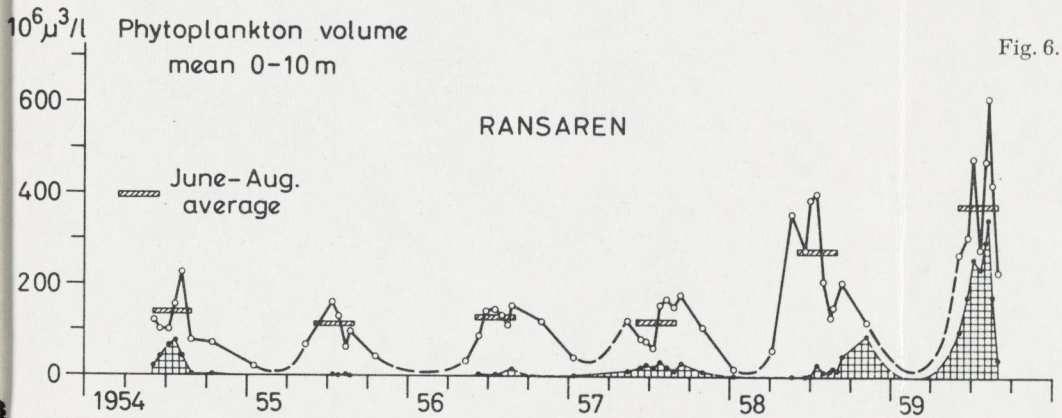
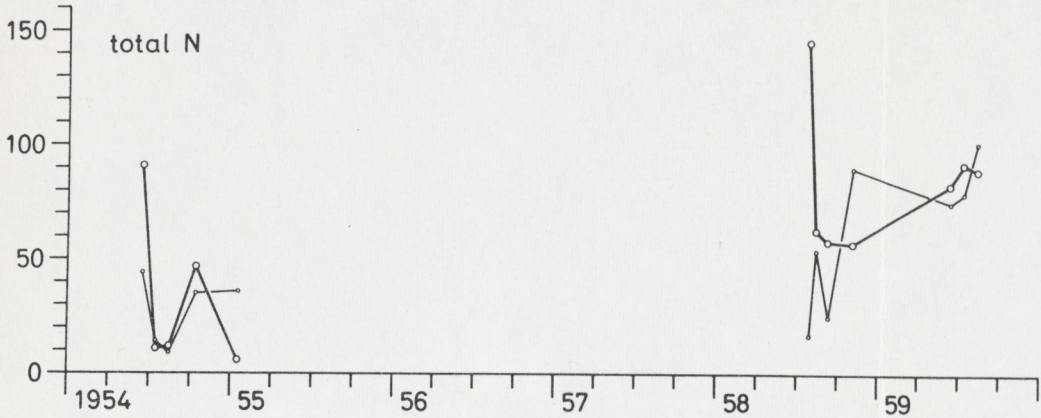
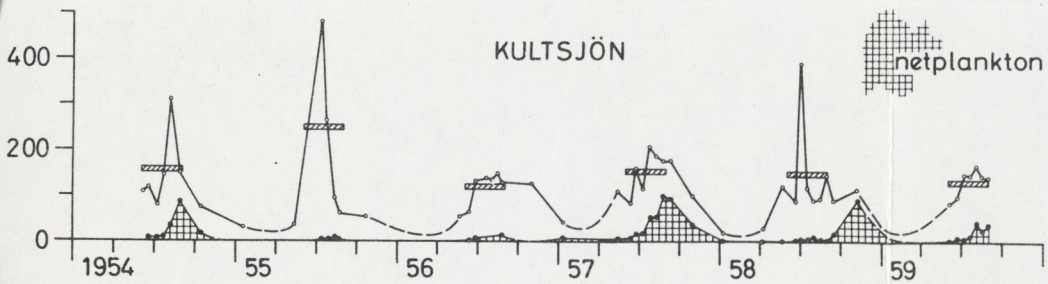
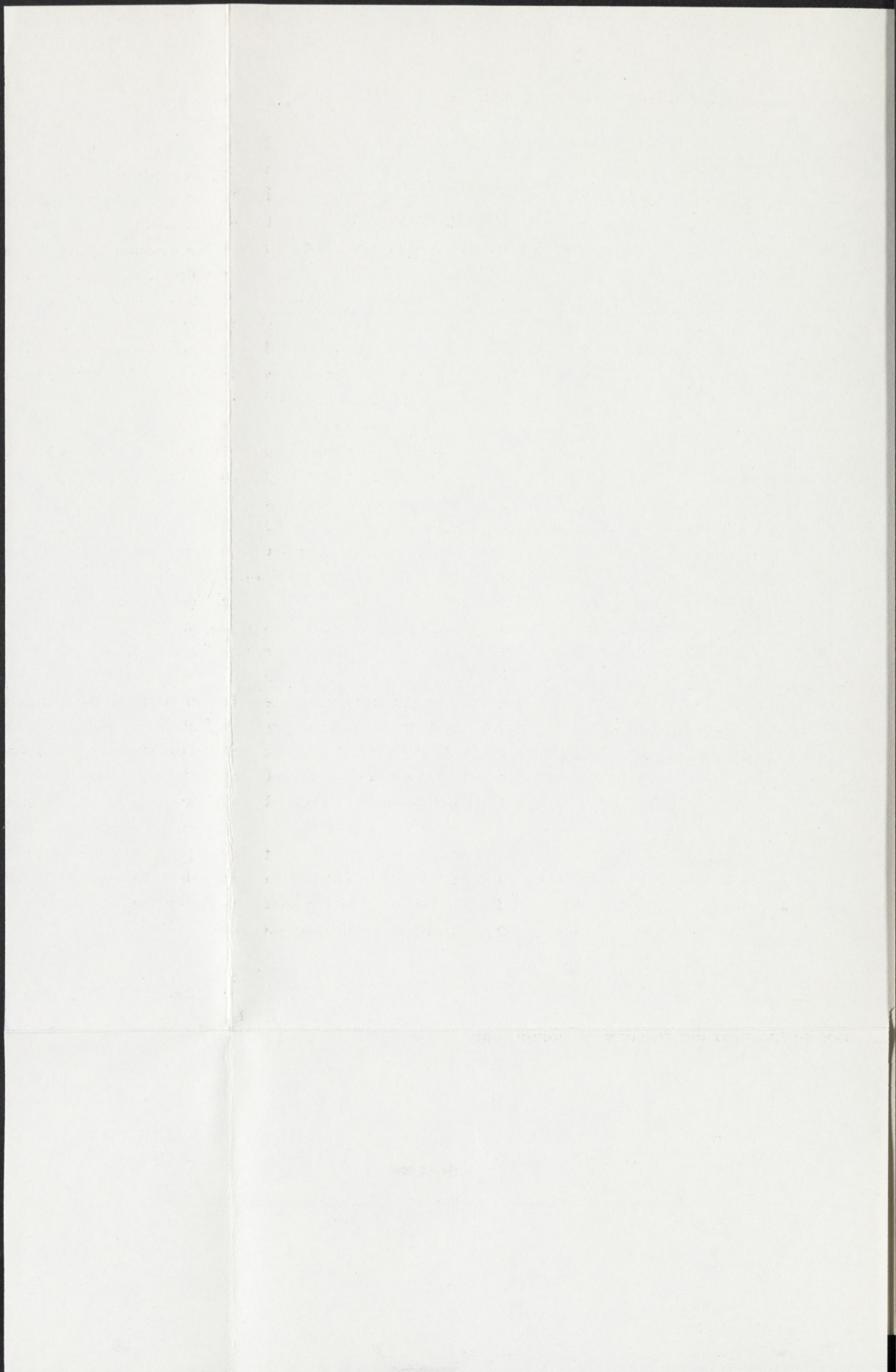


Fig. 6.





other pre-impoundment actions, but they were found in Kultsjön as well. In 1958, however, an early outburst raised the summer average to a level almost twice as high as in 1954 and 1955, despite a deep low in August which then was followed by another maximum, in the autumn. The step from 1958 to 1959 was not smaller than the previous one, giving a summer mean almost three times higher than was found in the first two years of the investigation.

The consistent increase of the total phytoplankton volume in Ransaren was accompanied by a distinct change in its composition, which had no equivalent in the phytoplankton of Kultsjön (Fig. 6). Details cannot be given here; suffice it to say that larger forms, such as *Dinobryon* and some diatoms, gained much importance in the impounded lake. This tendency resembles the qualitative shift in favour of net-plankton algae known to occur at slight eutrophication.

The primary production of organic matter was measured by means of carbon-14. The bottles were suspended for 24 hours at various depths in the trophogenic layer. As expected, the daily assimilation of inorganic carbon per unit lake area (Fig. 7) does correspond, roughly, to the algal biomass in the layer 0—10 m (Fig. 6). Thus no significant trend from year to year is seen for the primary production in Kultsjön, and Ransaren produced about three times more organic carbon in summer 1959 than it did in summer 1954.

In detail, however, the C^{14} -results diverge from the phytoplankton volumes. Most conspicuous are the differences for Ransaren in the years 1957 and 1958. Compared with the corresponding values from Kultsjön, the primary production — but not the standing crop, as just mentioned — in Ransaren was raised significantly even in 1957. In 1958, on the other hand, the summer mean for the primary production — but not for the phytoplankton — was lower than in the preceding year. In addition, the irregularities found in the course of the Ransaren curves for 1958 are much more pronounced for the production than for the algal biomass.

Some of these discrepancies and irregularities are due, no doubt, to wind-caused water movements within the lake, in particular internal seiches and horizontal displacement of epilimnic water (see further AXELSON 1961). Spatial heterogeneity sets many pitfalls to the interpretation of plankton and primary production profiles.

Zooplankton

A clear-cut response to the impoundment of Ransaren was manifested by its zooplankton. As can be seen in Fig. 8, the total zooplankton volume remained practically unchanged in Kultsjön throughout the whole period, and in Ransaren from 1954 to 1957 inclusive. After the first year of full impoundment and maximal winter discharge, however, the zooplankton of Ransaren reached, in the summer of 1958, population densities never recorded previously. Almost all species were involved in this sudden increase.

With the exception of one very high peak in the middle of July (consisting mainly of *Daphnia galeata* and *Cyclops scutifer*), the zooplankton volume in the summer of 1959, though higher than in the pre-impoundment years, was markedly lower than in 1958. This decrease was probably a consequence of the high summer discharge made in that year, which removed about a third of the epilimnion within a month. Because of the slower reproduction rate, the zooplankton seems to suffer more than the phytoplankton from such a withdrawal. Consequently, for zooplankton production in particular, the regulation routine ordinarily used (damming from spring to late autumn, discharge in winter) would be more favourable than the natural rhythm of water replacement in these lakes (highest discharge in spring and summer).

Conclusions

Prior to the impoundment proper, the dam construction and the burning of shore brush caused a transient increase of the phosphate level. To this fertilization only the primary production, not the algal biomass, responded with a clear but slight increase.

After the first full impoundment, however, the standing crop as well as the production of algae increased 2—3 times within two years, and so also did the zooplankton.

The increased productivity must have been caused mainly by a richer supply of nutrients from the flooded or, at low level, the eroded shores. It is, therefore, remarkable that the observed changes of the chemical conditions were quite small (phosphate, total phosphorus, total nitrogen) or absent (nitrate, major constituents).

It must be assumed that the surplus nutrients delivered to the lake were quickly assimilated. Thus the impoundment effects become more obvious in phyto- and zooplankton production and standing crops than in the environmental conditions in which the production occurred. In other words: during the first impoundment years, the flow of energy through the ecosystem is enlarged and accelerated without spectacular changes in its chemical basis.

It remains to be seen if a new equilibrium will be established some time after the first impoundment, or if the raised productivity will decline as indicated in other impounded lakes by observations on fish populations. According to the limited information available from July and August of 1960, neither primary production nor zooplankton continued to increase in Ransaren but had about the same levels as in the preceding summer.

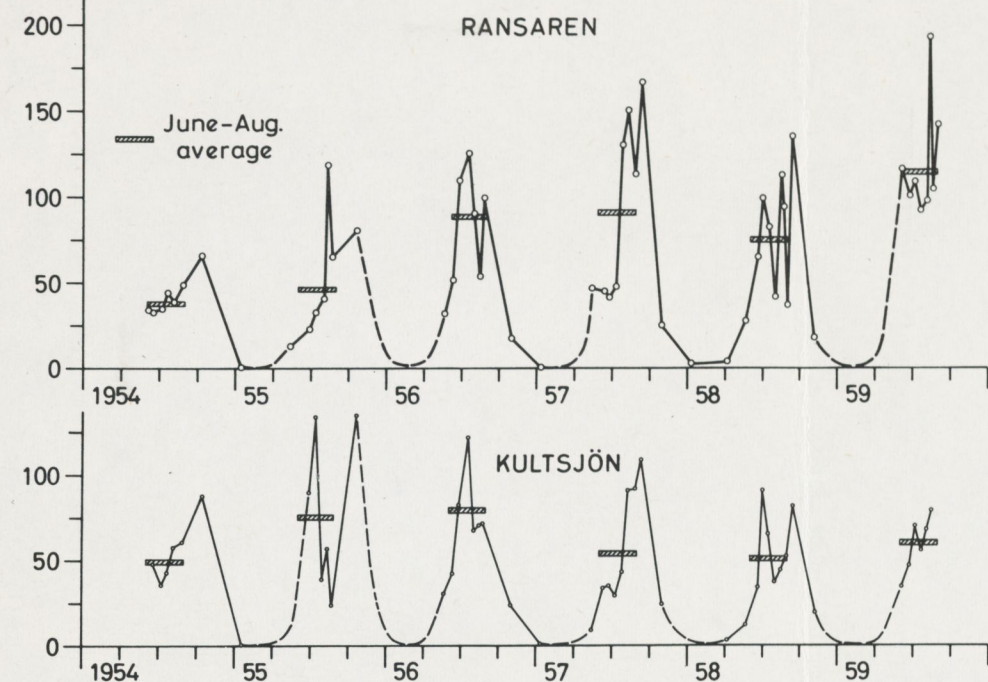
Discussion

PECHLANER: 1. Could greater quantities of detritus brought into the lake from flooded meadows and forests account for the larger standing crop of zooplankton? 2. Small nematodes, probably originating from the soil, are found swimming in alpine lakes that have just been made. Have you observed anything similar?

RODHE: 1. Yes. 2. Not as far as I know.

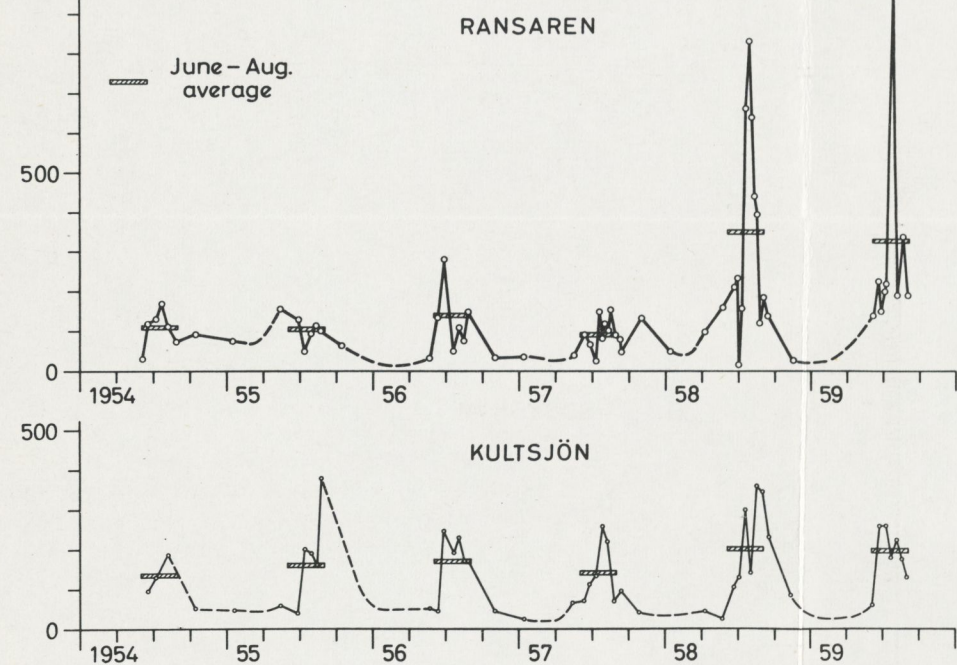
mgC_{ass}/m².d Primary production

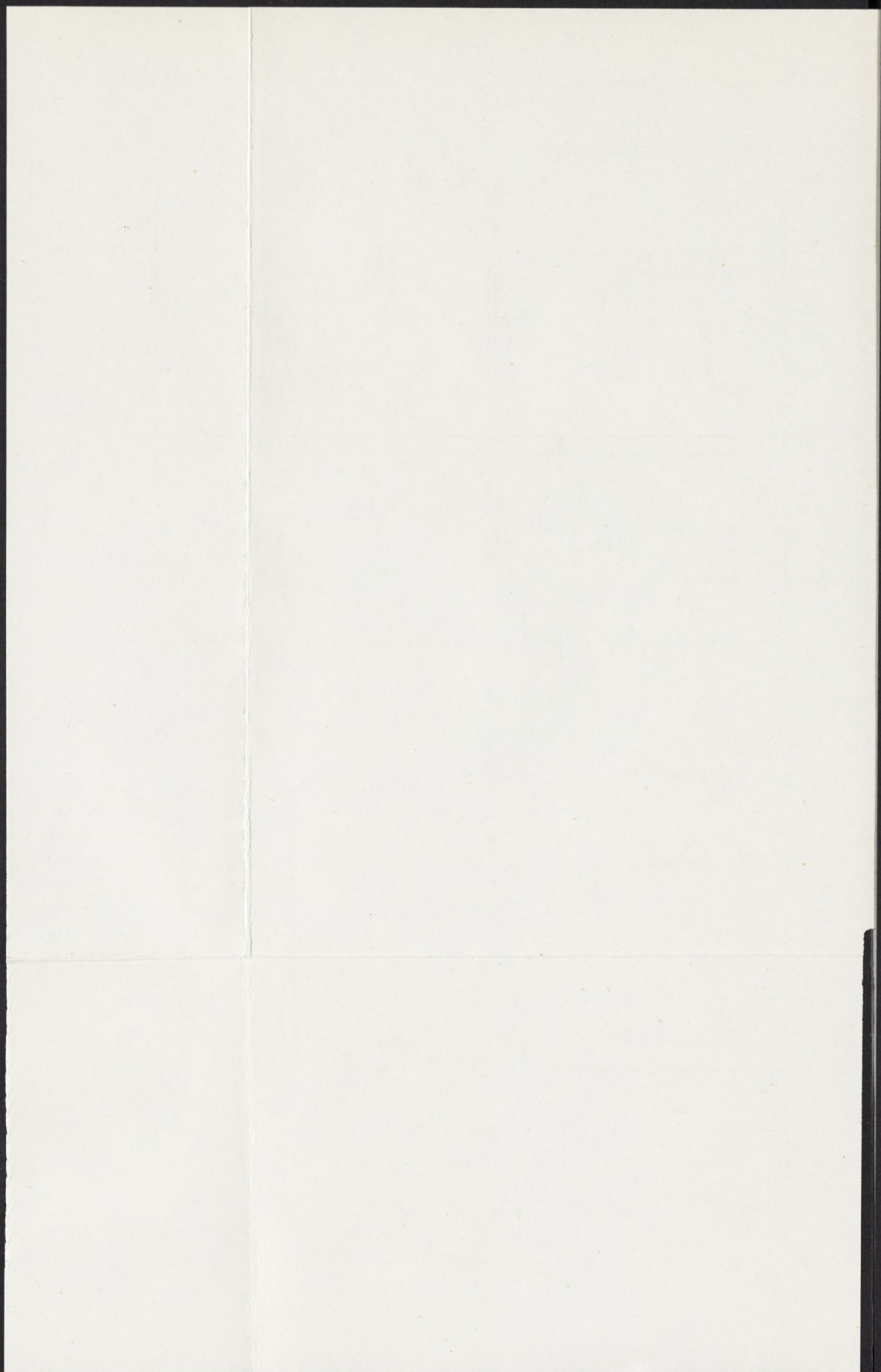
Fig. 7.



10⁶μ³/l Zooplankton volume mean 0-40 m

Fig. 8.





JOHNSON: During 1959 when zooplankton standing crop was lower, and attributable as you infer, to higher flushing rate, what was the rate of renewal of water?

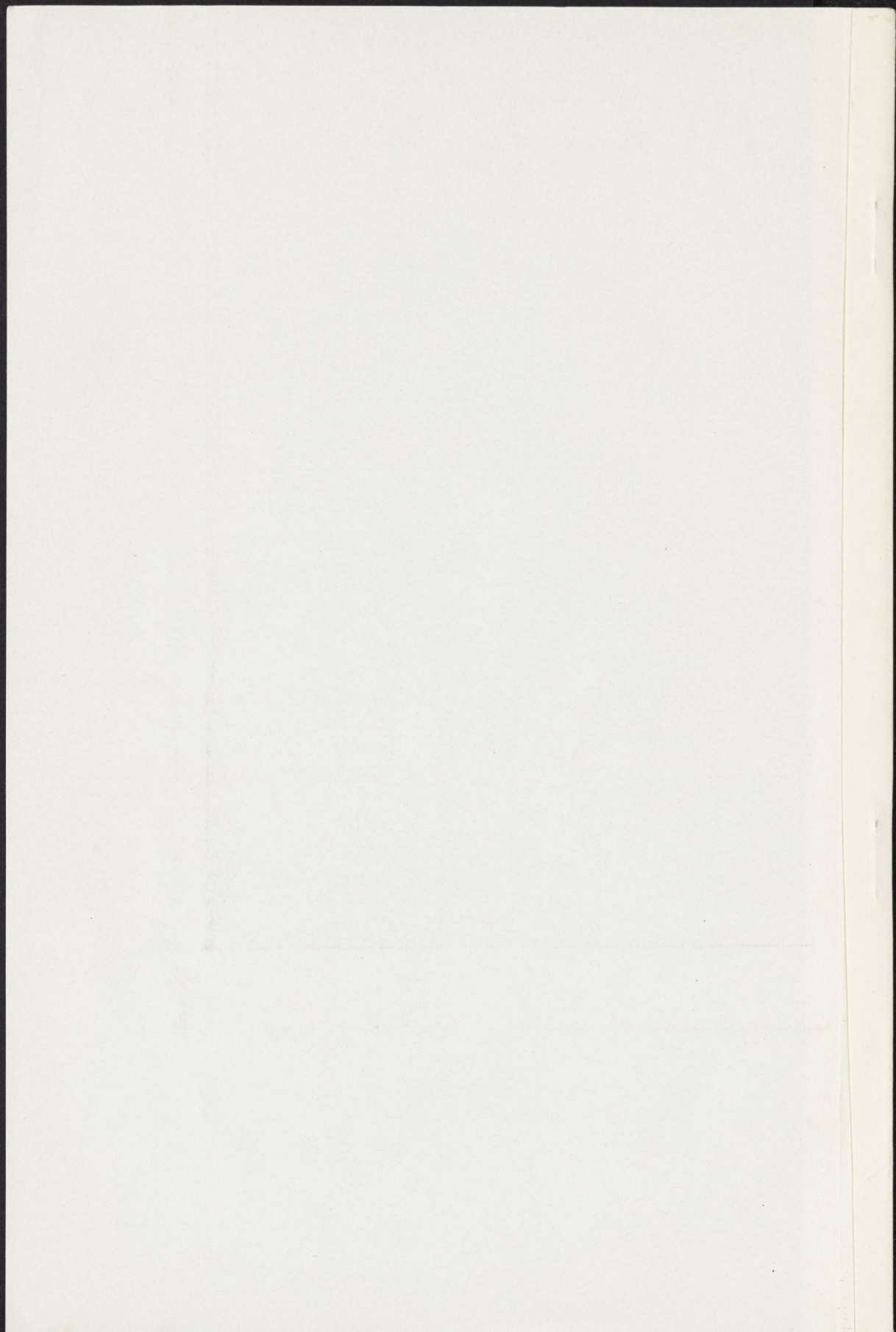
RODHE: Approximately 100 days.

DAMANN: What effect did impoundment have upon the water temperature?

RODHE: We did not observe any.

W. R. SCHMITZ: Do you plan to continue your observations of Lake Ransaren during the next few years, in spite of the fact that the control will be lost?

RODHE: Yes. We hope that funds will be available to continue.



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*Nutrient Regeneration from Phytoplankton Decomposing in Seawater*¹

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ABSTRACT

A laboratory model of the regeneration of the inorganic nutrient salts of phosphorus, nitrogen, and silicon from diatom cells decaying in the dark while subject to bacterial attack was studied. The system was analyzed for phosphate, dissolved and particulate organic phosphorus, ammonia, nitrite, nitrate, dissolved and particulate nitrogen, and orthosilicate concentrations. The observations extended over a period of more than one year, but the significant changes appear to have been restricted to the first five months.

Nitrogen remineralization, which did not go beyond ammonification, following an initial lag period, proceeded at a rate of 16:1, by atoms, relative to the rate of phosphorus remineralization. This experimental result is in close agreement with the hypothesis developed by Redfield (1934) from the relative distribution of nitrate and phosphate in the sea. Comparison of silica re-solution with phosphorus remineralization, however, did not confirm Richards' (1958) hypothesis, which was similarly derived from the relative distribution of phosphate and silicate in the sea.

A mechanism for phosphorus remineralization consisting of a simple first-order chain process was developed from kinetic considerations.

Introduction. The phosphates, nitrates, and silicates removed from solution and aggregated into organic particles by phytoplankton in the surface layers of the sea are subsequently returned to solution as dissolved inorganic salts through the metabolic activities of the marine community or by nonorganic, purely chemical transformations. The distribution of these elements, therefore, depends not only on physical processes but on the sinking and swimming of organisms and the mechanism and kinetics of the regeneration processes. Although the biochemical circulation (Redfield et al. 1963) results in nutrient distributions differing from those of the conservative salts, rather simple

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linear relationships exist between the concentrations of the biochemically active solutes. Redfield (1934) demonstrated that the changes in concentration of phosphate, nitrate, carbon dioxide, and oxygen in ocean waters normally occur in fixed relative proportions; this suggests that in the growth and decay of organisms these solutes are abstracted or returned to solution at constant relative rates.

The ratio of change of nitrate concentration relative to phosphate derived from Redfield's analysis, after correcting phosphates for salt error (Cooper 1938), is 15:1, by atoms; this is in reasonably good agreement with the 16:1 atomic ratio of nitrogen to phosphorus given by Fleming (1940) for average plankton. However, Riley (1951), employing a complex model of the Atlantic Ocean from which were obtained average rates of biological change for oxygen consumption and nitrate and phosphate regeneration at various sigma-t surfaces, found that the ratios of these rates of change varied greatly at the various sigma-t levels and were far from being constant, as Redfield's hypothesis implied.

In contrast to nitrogen and phosphorus remineralization, the re-resolution of silica from diatom tests is presumed to be a strictly inorganic hydrolytic process. However, Richards (1958) suggested that changes in dissolved silicate concentrations are linearly related to changes in phosphate and nitrate concentrations and oxygen consumption over intermediate depth ranges in the Caribbean Sea and in the Woods Hole-Bermuda region of the Atlantic. These facts were interpreted as indicating that silica re-resolution might be directly related to biological processes involved in nitrate and phosphate regeneration.

To test the hypothesis that the distribution of these nutrients in the sea is the result of simple, constant relationships between their regeneration rates, the latter were observed in a controlled laboratory experiment. The regeneration of silicon, phosphorus, and nitrogen have been studied individually by several workers (Cooper 1935, Hoffman 1956, von Brand et al. 1937, 1939, 1940, 1941, 1942, Lewin 1961, Jørgensen 1955), but none has observed them simultaneously. Since the flux of organic matter along all the branching food chains in the sea would be practically impossible to reproduce, it was decided to investigate the relatively simple case of re-resolution of phosphorus, nitrogen, and silicon from a crop of diatoms as it decayed in the dark and was subjected to bacterial attack.

Experimental Procedure. A 160-liter sample of seawater ($S = 33.12\text{‰}$) was pumped with an all-plastic pump from a depth of 100 m just west of Smith Island in the Strait of Juan de Fuca where relatively uncontaminated seawater could be obtained. The 200-liter polyethylene drum used as the experimental container had been scrubbed with 10% hydrochloric acid and rinsed with distilled water.

The drum was covered with clear Lucite^R (E. I. DuPont de Nemours & Co., Inc., Wilmington, Delaware). A stirrer and wall scrubber, consisting of a disk-shaped brush with polyethylene bristles attached to a Lucite handle, was so constructed that it could be rotated and moved vertically in the drum to stir the water and scrub the container.

The seawater was filtered through medium porosity filter paper (Eaton-Dikeman No. 613) and placed in a room thermostated at 11°C. A plankton inoculum, obtained by towing a no. 18 plankton net (ca. 0.08-mm aperture) in Puget Sound off Seattle, Washington, was added. Addition of 0.042 g potassium phosphate, dibasic salt, and 0.36 g potassium nitrate brought the nutrient concentrations to 3.6 $\mu\text{g-at PO}_4\text{-P/l}$ and 51 $\mu\text{g-at NO}_3\text{-N/l}$. The silicate concentration of the water was 54 $\mu\text{g-at Si/l}$. Sodium carbonate solution (2 M) was used to adjust the pH to 8.2. The sample was exposed to light from daylight-type fluorescent tubes that gave a total illumination of about 10,000 lux.

One month after inoculation, the phosphate concentration was reduced to 0.08 $\mu\text{g-at PO}_4\text{-P/l}$. Two days later the light was removed and the sample darkened by covering it with a sheet of black polyethylene. For all practical purposes, the population consisted of a pure culture of an unidentified centric diatom.

After darkening, subsamples were periodically withdrawn and analyzed for inorganic phosphate, total dissolved phosphorus, total phosphorus, ammonia, nitrite, nitrate, total organic nitrogen, soluble organic nitrogen, and silicate. Soluble material, specified here as that passed by a type HA Millipore^R (Millipore Filter Corp., Bedford, Mass.) with a 0.45- μ pore size, thus included material of colloidal size. Analyses for total phosphorus, ammonia, and total organic nitrogen were made on unfiltered water. All other samples were Millipore-filtered when collected. The walls and bottom of the drum were scrubbed and the water was thoroughly stirred prior to each sampling. The system never became anoxic and the pH varied between 8.1 and 8.2.

In general, the subsamples were frozen at the time of collection and stored until a convenient number had been collected for analysis. Inorganic phosphate samples were filtered, placed in glass-stoppered Pyrex^R bottles (Corning Glass Works, Corning, N. Y.), saturated with chloroform, and frozen. At the time of analysis, they were brought to room temperature and analyzed by the method of Wooster and Rakestraw (1951). Total dissolved phosphorus samples were filtered, transferred to Vycor^R flasks (Corning Glass Works, Corning, N. Y.), covered, and refrigerated. Unfiltered samples for total phosphorus determinations were similarly stored until analyzed by the acid hydrolysis technique (Harvey 1948). Particulate phosphorus was estimated as the difference between the total phosphorus and total dissolved phosphorus. Dissolved organic phosphorus was derived as the difference between the total dissolved phosphate fractions and the inorganic phosphate fractions.

Samples for ammonia and total organic nitrogen were collected without filtration in soft-glass bottles fitted with polyethylene-lined screw caps, acidified to a pH of about 4 with 10% hydrochloric acid, and stored frozen. At the time of analysis, samples for total organic nitrogen were first withdrawn. The remaining water was titrated with 1 N sodium hydroxide until alkaline to phenol red (pH 7-8). Ammonia was determined by the technique described by Riley (1953) and Riley and Sinhaseni (1957). Total organic nitrogen was determined by a micro-Kjeldahl method in which 10-ml samples were digested for 3-4 hours with 1 ml concentrated sulfuric acid and 5 mg mercuric oxide. After cooling, 10 ml of ammonia-free water were added, and the digest was treated with 5 N sodium hydroxide to a point just short of the methyl orange end-point, with stirring and cooling during the titration. The titration was completed with 1 N sodium hydroxide to the orange end point, and one additional drop, which turned the solution a light golden yellow, was added. The ammonia was then determined as above. All samples were analyzed in duplicate along with duplicate blanks consisting of 5 mg mercuric oxide plus 1 ml concentrated sulfuric acid, and the sample absorbance was corrected for the blank. The total organic nitrogen determination returns both the organic nitrogen and inorganic ammonia, and the result must be corrected for the latter. The precision of the organic nitrogen determination approximates $\pm 10\%$.

Dissolved organic nitrogen samples were filtered, stored, and then analyzed, as for total organic nitrogen, in duplicate. Since this method returns both the organic nitrogen and inorganic ammonia and, as there is generally some loss of ammonia during filtration under vacuum, it was necessary to run a separate ammonia blank on the water. Particulate nitrogen values were derived as the difference between the total organic and dissolved organic nitrogen.

Nitrite and nitrate samples were filtered, stored frozen in glass-stoppered Pyrex bottles, and analyzed by the methods of Barnes and Folkard (1951) and Mullin and Riley (1955a).

Silicate samples were filtered, stored frozen in polyethylene bottles, and analyzed by the method of Mullin and Riley (1955b). Particulate silicate was derived as the difference between the initial dissolved silicate and the dissolved silicate at the time of observation.

Discussion of Results. The results are given in Table 1 and Figs. 1, 2, and 3.

During the first few days in the dark a rapid interchange of phosphorus between the various fractions took place. During the last two days in the light the phosphate concentration rose from 0.08 to 0.30 $\mu\text{g-at/l}$ (sample 1), but in the next four days in the dark it dropped to 0.07 $\mu\text{g-at/l}$. The dissolved organic phosphorus, which was relatively high at the time of darkening

TABLE I. CHANGES IN NUTRIENT CONCENTRATION FOLLOWING DARKENING OF THE SYSTEM, EXPRESSED IN $\mu\text{g-at/l.}$

Sample No.	Time, Days	$\text{NO}_3^- \text{N}$	$\text{NO}_2^- \text{N}$	$\text{NH}_3^- \text{N}$	Dissol. Org. N	Partic. Org. N	$\text{PO}_4^{3-} \text{P}$	Dissol. Org. P	Partic. P	$\text{SiO}_4^{4-} \text{Si}$	Partic. Si
1	0	0.04	0.19	0.79	14.6	49.1	0.30	0.84	2.61	9.63	44.4
2	1	0.33	0.18	-	-	-	0.11	1.04	2.60	8.06	45.9
3	2	0.54	0.22	-	-	-	0.14	0.40	3.21	-	-
4	4	0.87	0.15	-	-	-	0.07	0.24	3.44	-	-
5	5	0.98	0.16	0.71	14.4	51.6	0.09	0.22	3.45	1.79	52.2
6	6	0.71	0.22	-	-	-	0.06	0.26	3.43	2.80	51.2
7	7	0.83	0.21	-	-	-	0.05	0.22	3.48	-	-
8	8	-	0.14	-	-	-	0.18	0.08	3.49	2.80	51.2
9	10	-	0.13	-	-	-	0.10	0.43	3.22	-	-
10	13	0.67	-	0.79	13.5	54.7	0.16	0.46	3.06	-	-
11	17	0.16	0.18	-	-	-	0.06	0.20	3.49	5.38	48.6
12	20	0.98	0.15	-	-	-	0.02	-	-	-	-
13	22	0.75	-	-	-	-	0.02	0.29	3.44	8.06	45.9
14	28	0.75	0.08	-	-	-	0.17	0.16	3.42	13.2	40.8
15	33	-	0.06	4.80	17.2	44.8	0.96	0.26	2.53	15.7	38.3
16	37	0.82	0.20	7.66	17.2	39.8	1.17	0.25	2.33	-	-
17	43	0.76	0.11	-	-	-	1.46	0.24	2.05	21.7	32.3
18	48	0.75	0.10	-	-	-	-	-	2.08	-	-
19	51	0.82	0.13	12.3	18.5	34.2	1.48	0.31	1.96	27.0	27.0
20	55	0.78	0.10	-	-	-	1.52	0.35	1.88	-	-
21	59	0.60	0.09	-	-	-	1.76	0.23	1.76	32.6	21.4
22	63	0.44	0.07	19.5	-	-	1.81	-	-	-	-
23	65	0.71	0.05	-	-	-	1.79	-	-	32.8	21.2
24	69	0.55	0.02	20.5	21.5	24.8	1.96	-	-	-	-
25	72	0.80	0.01	21.1	-	-	1.87	-	-	36.4	17.6
26	76	0.87	0.31	-	-	-	2.04	-	-	-	-
27	79	0.65	0.18	22.9	23.8	21.7	2.10	-	-	39.0	15.0
28	83	0.41	0.10	23.5	-	-	2.14	-	-	41.3	12.7
29	86	0.59	0.14	-	-	-	2.18	0.41	1.16	40.1	13.9
30	90	0.55	0.15	24.2	-	-	2.25	0.38	1.12	40.6	13.4
31	93	0.75	0.22	23.3	18.9	23.1	2.28	0.38	1.09	40.9	13.1
32	97	0.55	0.13	-	-	-	2.32	0.44	0.99	41.5	12.5
33	100	-	0.11	-	-	-	2.26	0.35	1.14	41.5	12.5
34	104	0.47	0.12	24.4	-	-	2.23	0.49	1.03	-	-
35	107	0.62	0.07	-	-	-	2.33	0.39	1.03	43.5	11.5
36	114	0.35	0.05	23.2	21.0	21.7	2.31	0.39	1.05	44.2	9.8
37	119	0.68	0.21	-	-	-	2.33	0.58	0.84	-	-
38	126	0.63	0.12	22.8	-	-	2.37	0.37	1.01	48.2	5.8
39	136	0.73	0.11	22.1	19.6	26.9	-	-	0.88	48.0	6.0
40	152	0.37	0.04	-	-	-	2.38	0.49	0.88	47.9	6.1
41	163	-	0.16	23.3	-	-	2.48	0.09	1.18	-	-
42	176	0.37	0.16	-	-	-	2.46	0.17	1.12	52.1	1.8
43	191	0.73	0.14	-	-	-	2.44	0.20	1.11	55.2	-

(Cont.)

TABLE I. (Cont.)

Sample No.	Time, Days	NO ₃ ⁻ -N	NO ₂ ⁻ -N	NH ₃ -N	Dissol. Org. N	Partic. Org. N	PO ₄ ⁻³ -P	Dissol. Org. P	Partic. P	SiO ₄ ⁻⁴ -Si	Partic. Si
44	204	0.15	0.14	21.5	-	-	2.46	0.21	1.08	53.8	0.2
45	226	0.31	0.12	21.6	19.0	24.5	2.36	0.23	1.16	52.6	1.4
46	247	0.30	0.12	24.5	-	-	-	-	-	54.1	-
47	280	0.15	0.05	22.8	-	-	2.34	0.36	1.05	55.3	-
48	348	0.64	0.05	20.7	20.3	25.5	2.40	0.13	1.22	54.4	-
49	377	-	0.07	-	-	-	2.41	0.14	1.19	-	-
50	414	0.44	0.06	22.9	19.4	25.3	2.40	-	-	-	-

TOTAL PHOSPHORUS CONCENTRATION - 3.75 $\mu\text{g-at P/l}$.

TOTAL SILICON CONCENTRATION - 54.0 $\mu\text{g-at Si/l}$.

(0.84 $\mu\text{g-at/l}$), increased to more than 1.0 $\mu\text{g-at/l}$ by the following day and then rapidly decreased. The particulate phosphorus remained constant the first day, but by the third sampling it had increased markedly and reached maximal concentrations by the fourth day.

The increase of inorganic phosphate during the final two days in the light and the high concentration of dissolved organic phosphorus found in the initial

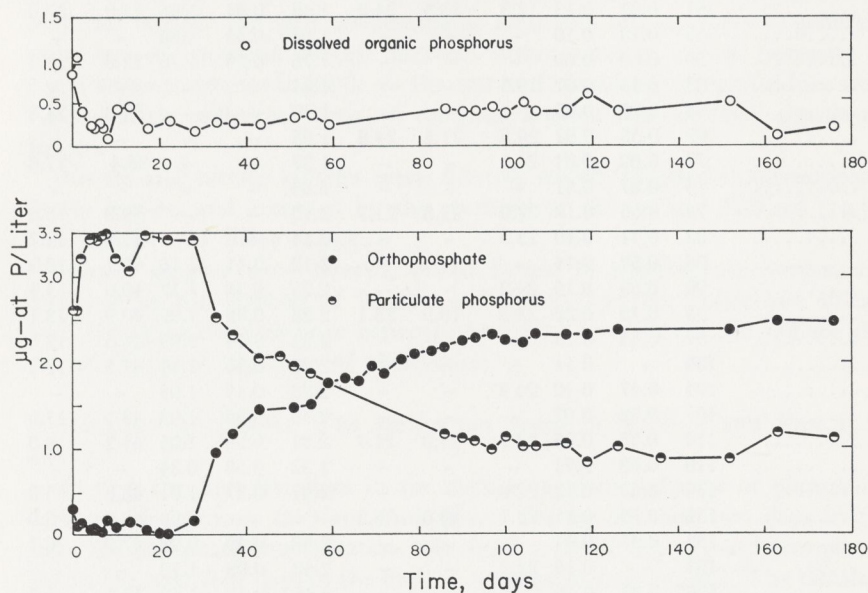


Figure 1. Phosphorus concentrations after the system was darkened.

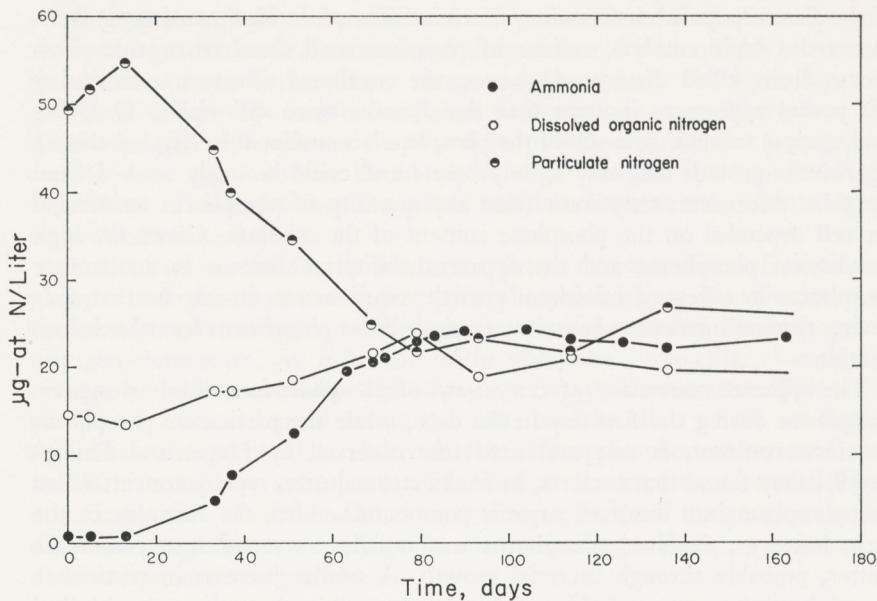


Figure 2. Nitrogen concentrations after the system was darkened.

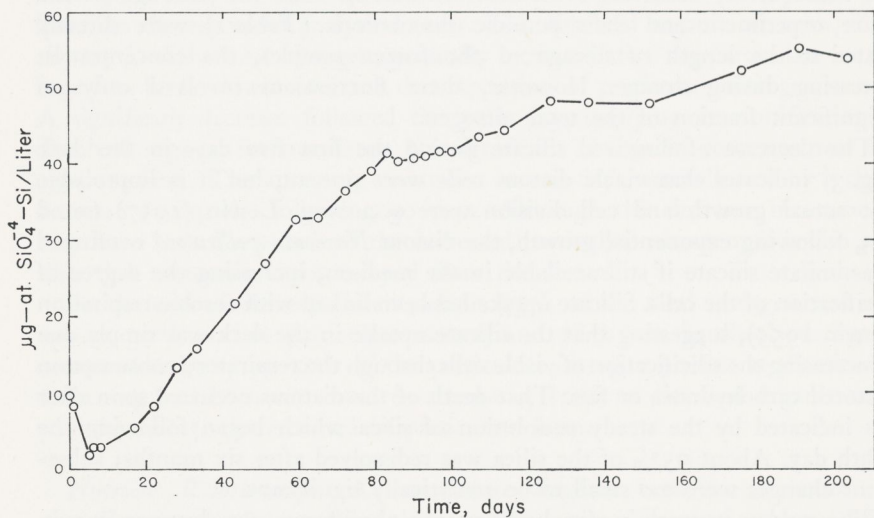


Figure 3. Dissolved silicate concentrations after the system was darkened.

sample could be interpreted as the onset of death and autolytic decomposition of the diatom population following nutrient exhaustion. Hoffman (1956) demonstrated a rapid autolytic release of phosphate and dissolved organic phosphorus from killed diatoms. However, the continued silicate uptake during this period appears to indicate that the diatoms were still viable. Goldberg et al. (1951) found that much of the phosphate accumulated by diatoms during logarithmic growth was only loosely bound and could be easily washed from the cells. Moreover, they found that the quantity of phosphorus assimilated per cell depended on the phosphate content of the medium. Given the high mobility of phosphorus and the apparent ability of diatoms to accumulate phosphorus in excess of minimum growth requirements, it may be that, following general nutrient exhaustion, excess cellular phosphorus leaks back into solution.

The apparent conversion of $0.2 \mu\text{g-at/l}$ of phosphate into dissolved organic phosphorus during the first day in the dark, while the particulate phosphorus remained constant, is comparable to that observed by Hayes and Phillips (1958); they found that bacteria, in freshwater cultures, rapidly convert added radiophosphate into dissolved organic compounds. After the first day in the dark, however, dissolved phosphorus was rapidly converted into particulate matter, probably through bacterial growth. A similar increase in particulate organic nitrogen occurred (Fig. 2), but it was within the estimated analytical error and, as the dissolved organic and inorganic nitrogen fractions showed no corresponding decrease, the increase is suspect. There was a small nitrate increase during the first few days (Table 1), but none of comparable magnitude was subsequently observed. Nitrite concentrations were low throughout the entire experiment and their periodic fluctuations (Table 1) were directly related to the length of storage of the frozen samples, the concentration increasing during storage. However, these fluctuations involved only an insignificant fraction of the total nitrogen.

The decrease of dissolved silicate during the first five days in the dark (Fig. 3) indicates that viable diatom cells were present, but it is improbable that actual growth and cell division were occurring. Lewin (1957) found that, following exponential growth, the diatom *Navicula pelliculosa* continued to assimilate silicate if still available in the medium, increasing the degree of silicification of the cells. Silicate uptake has been linked with aerobic respiration (Lewin 1955), suggesting that the silicate uptake in the dark was simply due to increasing the silicification of viable cells through the respiratory consumption of stored carbohydrates or fats. That death of the diatoms occurred soon after was indicated by the steady re-resolution of silica which began following the eighth day. About 95% of the silica was redissolved after six months; subsequent changes were too small to be analytically significant.

The sudden increase in dissolved organic phosphorus, the decrease in particulate phosphorus, and the onset of silica re-resolution after the eighth day

suggest the autolytic release of dissolved organic phosphorus compounds from a dying diatom population, similar to that described by Hoffman (1956). A rapid bacterial multiplication apparently followed and quickly consumed the dissolved organic phosphorus compounds, so that by the 17th day they had been completely reassimilated into particulate matter. Thereafter, the dissolved organic phosphorus fluctuated irregularly and, on the average, increased at an approximately linear rate through the first four months of the experiment. This trend then leveled off until the sixth month, when a significant decrease took place.

At the end of the fourth week, an abrupt decomposition of particulate phosphorus and an increase in inorganic phosphate began. By this time particulate nitrogen had begun to break down into ammonia and dissolved organic nitrogen compounds. An inflection in the phosphate curve (Fig. 1) at day 55 corresponds almost precisely with Cooper's (1935) observations. Thereafter, phosphates increased until about the fifth month, after which no further significant change could be detected. Particulate phosphorus decreased until the fifth month but subsequently increased at the expense of the dissolved organic fraction. At the end of the experiment, 64% of the phosphorus was dissolved inorganic phosphate, 32% was particulate, and 4% was bound in dissolved organic compounds.

Particulate nitrogen began to break down into ammonia and dissolved organic compounds after the second week. Ammonia increased at a decreasing rate during the next three months and reached a maximum after 104 days. The particulate nitrogen decreased for about 60 days, leveled off for the following 40 days, and then appeared to increase slightly, but the increase was less than the estimated analytical error. The dissolved organic nitrogen, initially 23% of the total nitrogen, gradually increased after the particulate matter began to break down until the decomposition of particulate nitrogen ceased. A significant decrease followed the 79th day, implying ammonification of dissolved organic intermediates. No significant change in concentration was apparent later. The ammonia maximum at 104 days was followed by a slight decrease during the following 30 days. Although this decrease in ammonia may have been the source of the increased particulate nitrogen, it is also possible that ammonia vapor escaped from the system.

At the end of the experiment, about 33% of the total nitrogen was ammonia, 39% was in particulate matter, and 28% was in dissolved organic compounds. Forty per cent of the particulate nitrogen present at the time of darkening had been converted to ammonia, 10% to dissolved organic compounds, and 50% remained in particulate form.

Nutrient Relationships. A correlation diagram between ammonia and phosphate concentrations (Fig. 4) shows that between days 33 and 104, when the greater portion of the nutrients was remineralized, ammonia and phosphate

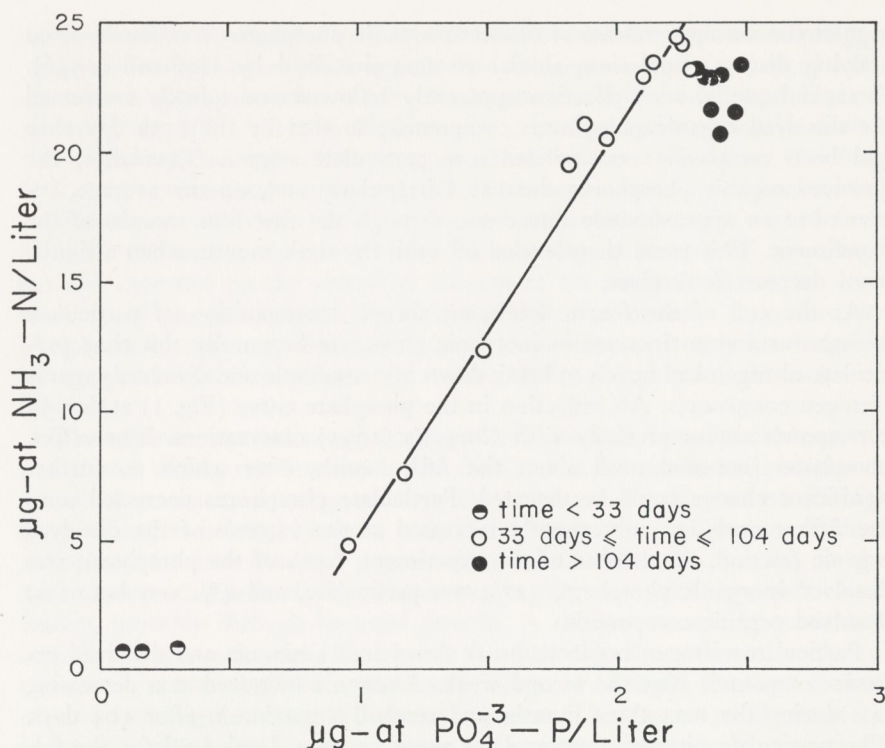


Figure 4. Correlation diagram between ammonia and ortho phosphate concentrations. The solid line represents the 16:1 rate of ammonification relative to phosphate remineralization observed between days 33 and 104.

concentrations were reasonably well related by a simple linear expression. The slope $\Delta N:\Delta P = 16:1$, by atoms, indicates a rate of ammonification relative to phosphate remineralization of 16:1. However, prior to day 33 there was a rapid release of phosphate with little or no increase in ammonia, and following day 104 the ammonia concentration decreased without a corresponding decrease in phosphate. Dismissing the relatively small changes following day 104, it appears that the remineralization occurred in at least two distinct phases—an initial phase where there was a rapid release of phosphate alone, and a second phase during which phosphorus and nitrogen were remineralized at constant relative rates.

The 16:1 ratio maintained during the main phase of remineralization is of interest because of its close correspondence to the ratio in which nitrate concentrations in the sea are generally observed to change relative to phosphate (Redfield 1934, Cooper 1938). Nitrification was not realized during the experiment, but if ammonia and phosphate are released to the water from

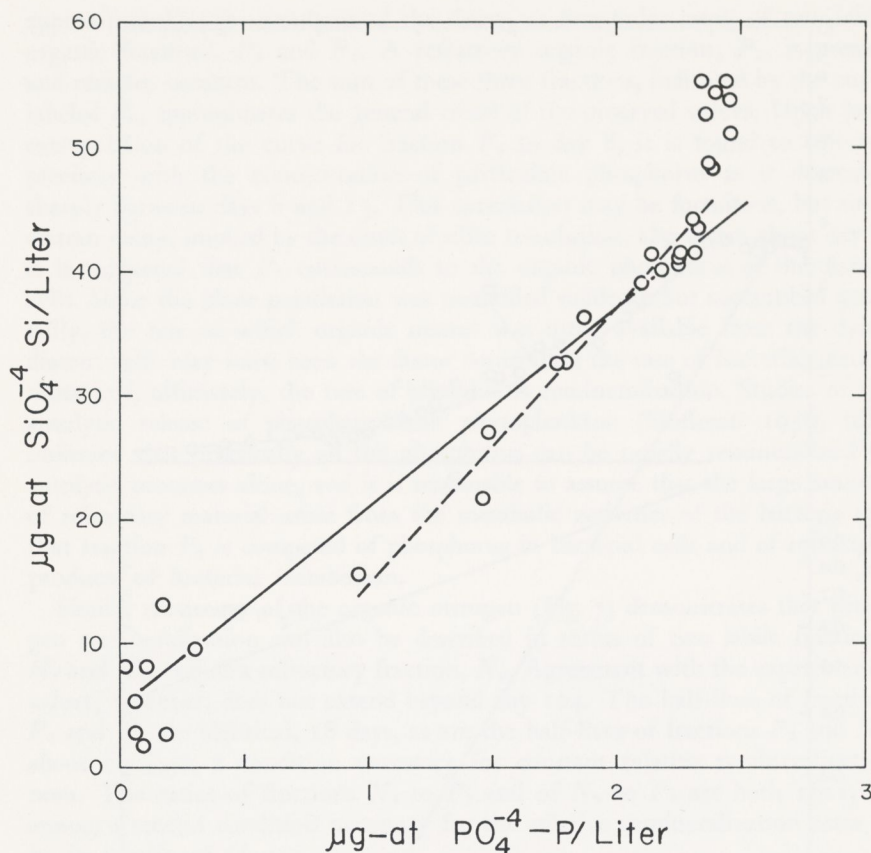


Figure 5. Correlation diagram between orthosilicate and orthophosphate concentrations. The solid curve represents the 16:1 relationship suggested by Richards (1958). The dashed curve represents a 23:1 relationship which appears to be better maintained among concentrations in an intermediate range.

sinking debris in this ratio, then, in the presence of the appropriate nitrifying bacteria, the proper nitrate-phosphate distributions could be obtained. However, mixing processes, if sufficiently rapid, could diffuse ammonia and phosphate differently and lead to anomalous nitrate-phosphate distributions.

The deviations from the 16:1, by atoms, silicate-to-phosphate regeneration ratio suggested by Richards (1958) are obvious from the correlation diagram (Fig. 5, solid line). There was, however, an approximately linear relationship in an intermediate concentration range, where the rate of change of silicate relative to phosphate is about 23:1, by atoms (Fig. 5, dashed line).

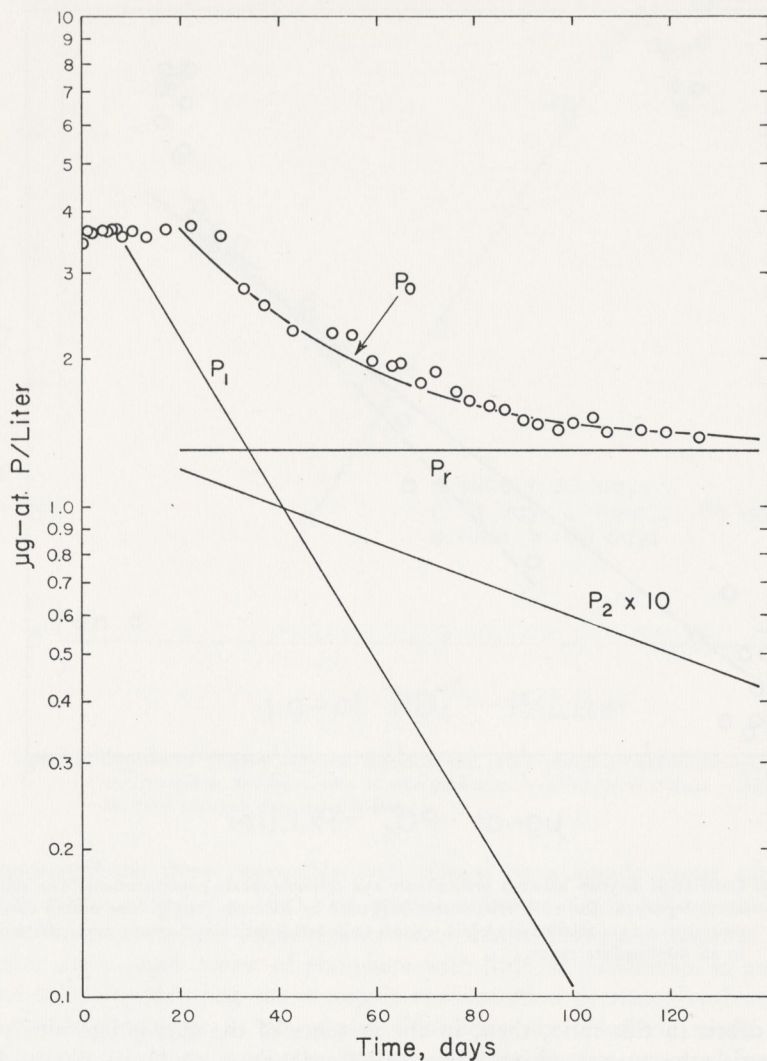


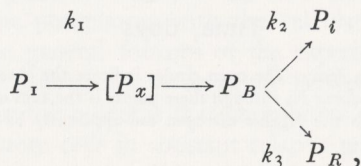
Figure 6. Analysis of phosphorus decay. The open circles indicate the observed total organic phosphorus in the system. The curve P_0 through these points is the sum of P_1 , P_2 , and P_r , the three fractions into which the organic phosphorus can apparently be decomposed.

Kinetic Model. In an effort to develop a simple model of these processes, the data have been examined for kinetic relationships. Upon plotting total organic phosphorus along a logarithmic ordinate against an arithmetic time abscissa (Fig. 6), it becomes apparent that phosphorus remineralization can be

approximated as the resultant of the decay, at first-order rates, of two labile organic fractions, P_1 and P_2 . A refractory organic fraction, P_r , is present and remains constant. The sum of these three fractions, indicated by the curve labeled P_0 , approximates the general trend of the observed values. Upon back extrapolation of the curve for fraction P_1 to day 8, it is found to coincide precisely with the concentration of particulate phosphorus as it decreased sharply between days 8 and 13. This correlation may be fortuitous, but since diatom decay, implied by the onset of silica re-solution, also began about day 8, it is suggested that P_1 corresponds to the organic phosphorus of the diatom cells. Since the plant population was not killed suddenly but succumbed gradually, the rate at which organic matter was made available from the dying diatom cells may have been the factor controlling the rate of bacterial metabolism and, ultimately, the rate of phosphorus remineralization. Studies of the autolytic release of phosphate from phytoplankton (Hoffman 1956) have indicated that practically all the phosphorus can be rapidly remineralized by autolytic processes alone, and it is reasonable to assume that the large amount of refractory material arose from the metabolic activities of the bacteria and that fraction P_r is composed of phosphorus in bacterial cells and of refractory products of bacterial metabolism.

Similar treatment of the organic nitrogen (Fig. 7) demonstrates that nitrogen remineralization can also be described in terms of two labile fractions, N_1 and N_2 , and of a refractory fraction, N_r . Agreement with the experimental values, however, does not extend beyond day 104. The half-lives of fractions P_1 and N_1 are identical, 18 days, as are the half-lives of fractions P_2 and N_2 , about 80 days, a condition necessary for constant relative remineralization rates. The ratios of fractions N_1 to P_1 and of N_2 to P_2 are both 16:1, by atoms, a second condition necessary for the relative remineralization rates to be in a ratio of 16:1.

Although biological processes cannot be expected to follow kinetic laws precisely, it has been possible to reconstruct the main features of the experimental observations by assuming that decomposition proceeds as a simple first-order chain reaction. The assumed mechanism, for phosphorus, is,



where P_1 is identical to fraction P_1 of Fig. 6 and is assumed to represent the phosphorus in diatom tissue. P_1 decays at a first-order rate described by its rate constant, k_1 . P_x is placed in the chain to recognize that phosphorus, in either organic or inorganic form, is released from the diatom fraction into

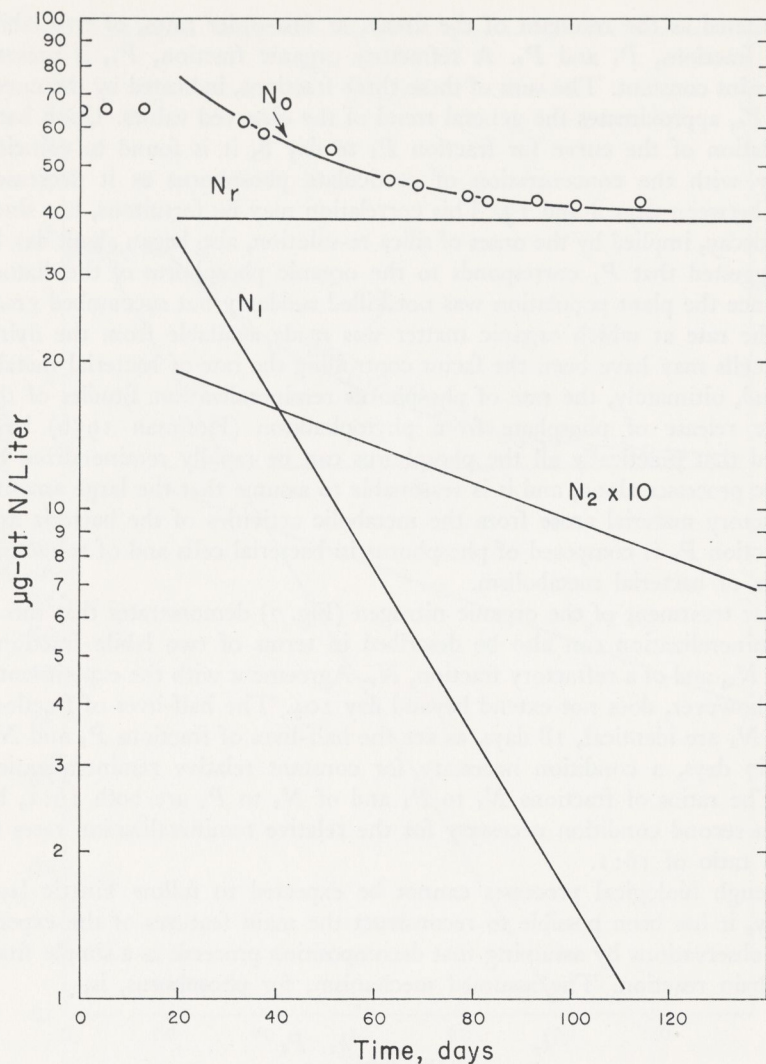


Figure 7. Analysis of nitrogen decay. The open circles indicate the observed total organic nitrogen in the system. The curve N_0 through these points is the sum of N_1 , N_2 , and N_r , the three fractions into which the organic nitrogen can apparently be decomposed.

the system before being accumulated by the bacterial fraction, P_B . However, the rate of bacterial assimilation appears to be so rapid that the concentration of P_x is always negligible. Bacterial respiration and the decay of dead bacterial cells give rise to fraction P_i , inorganic phosphate, and to P_R , the refractory organic substances released during bacterial metabolism and the undecomposed

remains of dead bacterial cells. The sum $(k_2 + k_3)$ describes the rate of loss of phosphorus from the bacterial fraction to the two product fractions formed in constant relative proportions.

The equations governing the model are

$$\begin{aligned}\frac{dP_I}{dt} &= -k_1 P_I, \\ \frac{dP_B}{dt} &= k_1 P_I - (k_2 + k_3) P_B, \\ \frac{d}{dt} (P_i + P_R) &= (k_2 + k_3) P_B;\end{aligned}$$

these have the solutions

$$\begin{aligned}P_I &= P_I^0 \exp[-k_1(t - t_0)], \\ P_B &= \frac{k_1}{(k_2 + k_3) - k_1} P_I^0 \{ \exp[-k_1(t - t_0)] - \exp[-(k_2 + k_3)(t - t_0)] \} \\ &\quad + P_B^0 [\exp-(k_2 + k_3)(t - t_0)], \\ (P_i + P_R) &= \Sigma P - (P_I + P_B), \\ P_R &= \frac{k_3}{k_2 + k_3} [(P_i + P_R) - (P_i^0 + P_R^0)] + P_B^0;\end{aligned}$$

P_I^0 , P_B^0 , P_i^0 , and P_R^0 are the concentrations of the respective fractions at the origin of time, t_0 ; these have the following values expressed in $\mu\text{g-at P/l}$: $P_I^0 = 3.50$, $P_B^0 = 0.00$, $P_i^0 = 0.05$, $P_R^0 = 0.20$, $t_0 = 8$ days.

ΣP is the total phosphorus in the system, $3.75 \mu\text{g-at/l}$. The value of k_1 , 0.0380 day^{-1} , was obtained from Fig. 6. The values of k_2 , 0.0381 day^{-1} , and k_3 , 0.0174 day^{-1} , were derived empirically, essentially by trial and error, to determine if a set of first-order rate constants could be found to give a curve that would fit the observations reasonably well. Fig. 8 illustrates the results of computation using the above equations and constants and compares the observed total organic phosphorus with the calculated values. Although the model reproduces the general features of the experimental results reasonably well, an appreciable discrepancy is apparent between days 15 and 33. An assumption implicit in the model is that phosphorus and oxidizable carbon are released from the diatom cells in constant relative proportions throughout the experiment. If, however, during this initial phase, a substrate relatively rich in oxidizable carbon was being metabolized, it might be necessary for the bacteria to draw upon phosphate from the medium. This possibility is suggested by the findings of Guillard and Wangersky (1958) that senescent diatom cultures, in bacteria-free media, may release dissolved carbohydrates.

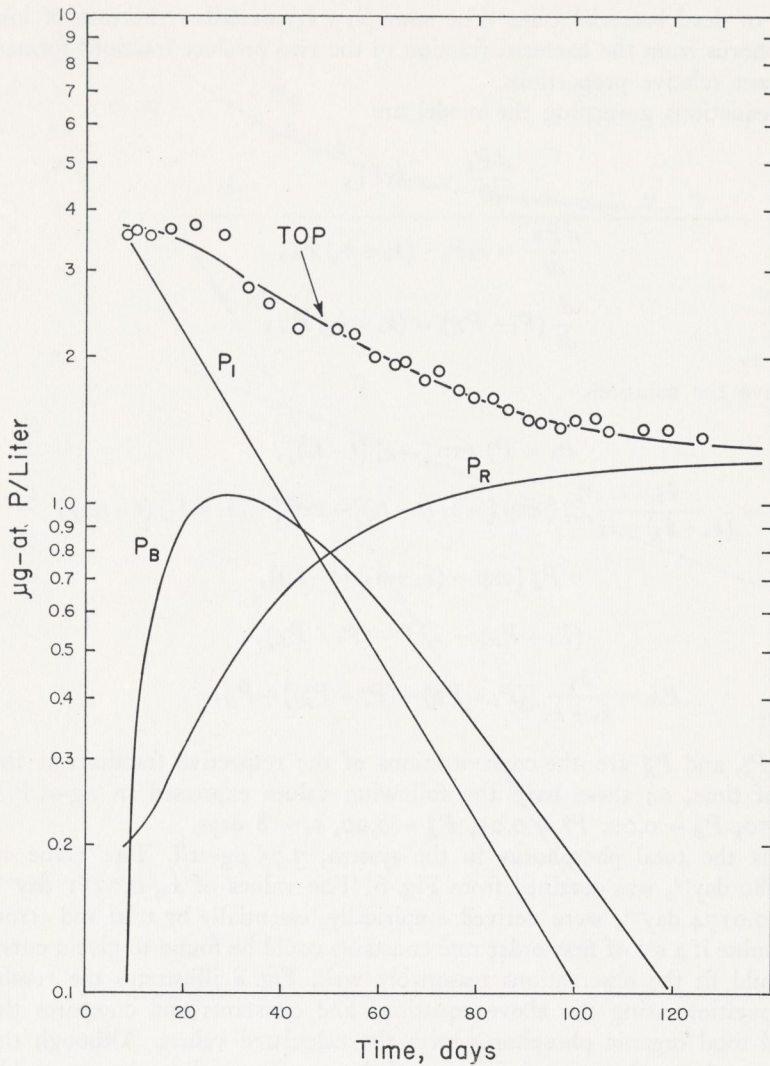


Figure 8. Model of phosphorus decay. The open circles indicate the observed total phosphorus in the system. The curve, TOP, through the points is the sum of fractions P_I , P_B , and P_R .

A similar model of nitrogen decay could be prepared, but the effort would be difficult to justify with the experimental observations available. Mineralization of nitrogen is probably more complex than that of phosphorus because of the greater number of intermediates possible between protein and ammonia. The changes in the dissolved organic nitrogen fraction seem to be evidence

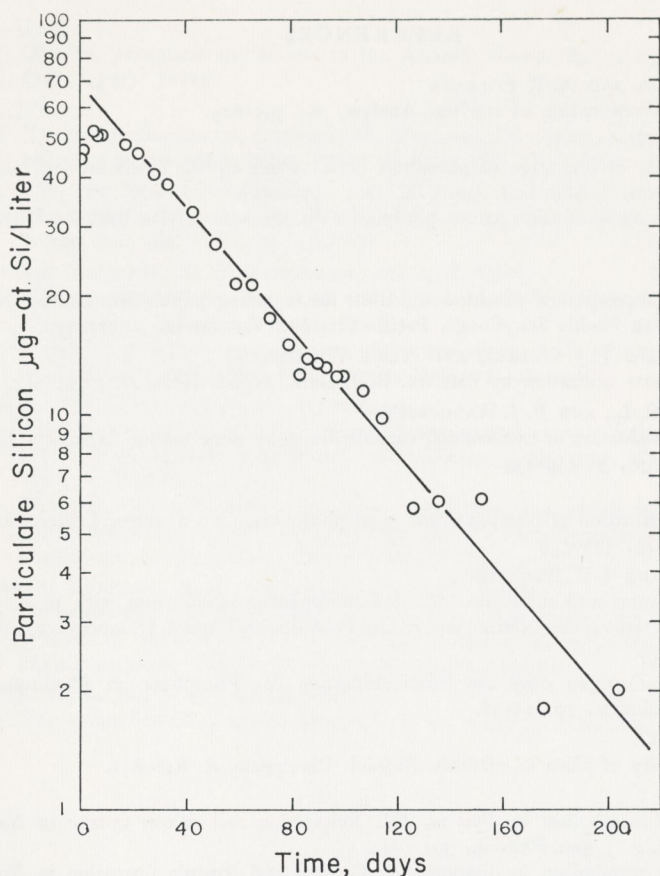


Figure 9. Analysis of silica decay.

of such intermediates. The formation and decomposition of such intermediates would retard the appearance of the end product while the intermediates built up to equilibrium concentrations. While there is evidence of the accumulation of nonrefractory dissolved organic nitrogen intermediates, there is none of an accumulation of similar organic phosphorus intermediates. Such factors could be responsible for discrepant remineralization ratios during the initial stages of the process.

Analysis of silica re-solution (Fig. 9) indicates that it too can be represented as a simple first-order process. The re-solution rate was 0.017 day^{-1} .

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RELATIONSHIP OF HERBIVORE GROWTH TO RATE OF GROSS PHOTOSYNTHESIS IN MICROCOSMS¹

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ABSTRACT

Tilapia mossambica (Peters) fry were reared in tank microcosms on the proceeds of *in situ* algal photosynthesis only. The cube root of average rate of individual weight gain was related linearly to average rate of gross photosynthesis. Failure of increased population density to suppress individual growth rate was attributed to inefficient foraging and rapid decomposition of uneaten settled phytoplankton.

INTRODUCTION

Experiments were undertaken to understand how fish production is related to primary productivity. The importance, and some difficulties, of evaluating criteria of potential fish productivity in lakes has been discussed by McConnell, 1963. The relationship between gross photosynthesis and potential fish production is best examined under natural conditions, but waters in which this can be done meaningfully are rare. Microcosms offer a way of supplementing the infrequent opportunities of studying the problem in nature.

EXPERIMENTAL CONDITIONS

Tilapia mossambica (Peters) fry were reared on the food produced by photosynthesis in 16 microcosms. Microcosm containers were galvanized steel tanks. Each tank in the numbered series had a volume of 310 liters and a surface area of 0.62 m². Tanks used in experiments A through E contained 2,840 liters in use and had a surface area of 2.12 m². Depths were 0.50 m and 1.35 m. All tanks were coated with a zinc-filled epoxy primer and two coats of clear epoxy resin. A curing period was followed by prolonged overflow rinsing before the tanks were filled with tap water for the experiments.

A gradient of rates of photosynthesis was established by adding graded amounts of

phosphoric acid and calcium nitrate. The tap water contained about 2 mg/liter of nitrate, 20 mg/liter of sulfate, 120 mg/liter of calcium bicarbonate, and a wide variety of other salts in trace quantities. Including the nitrate initially present in tap water and that added, nitrogen application ranged from the equivalent of 8 kg/hectare in some tanks to a high of 170 kg/hectare in others. Applications of phosphorus ranged from an amount equal to 0.023 kg to 340 kg/hectare. The 2,840-liter tanks also received the equivalent of 29 kg/hectare of potassium and supplements of the recognized minor nutrient salts. Scheduled nutrient salt additions were increased or decreased to maintain photosynthetic rates at desired levels.

Inoculating plankton organisms

A variety of plankton organisms was inoculated in the tanks by adding about 100 ml of a mixture of water from other established tanks and from ponds and lakes near Tucson. There was little relationship between kinds of organisms dominant in the inoculum and those that became dominant in the tanks. No two tanks contained the same types of communities simultaneously; however, during the course of the experiment a similar array of producer organisms appeared in all. The phytoplankton was composed mostly of chlorophyceans including *Oocystis* sp., *Scenedesmus* sp., and several unidentified coccoid forms. Filamentous algae were rare except for a mixture of blue-green forms appearing in the *Aufwuchs*. The *T. mossambica* apparently prevented the development of macroinvertebrates. Rotifers

¹Contribution from the Arizona Cooperative Wildlife Research Unit. Financial support was provided by Arizona Game and Fish Department through Federal Aid to Fisheries Project F-8-R, and by the University of Arizona.

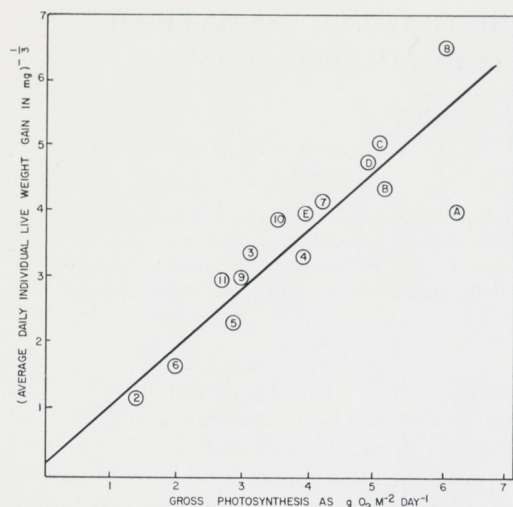


FIG. 1. Relation of *T. mossambica* growth rate to rate of gross photosynthesis. Figures refer to experiments described in text and tables.

and ciliates were always present in all tanks but neither were ever abundant.

T. mossambica introduction

T. mossambica fry averaging about 12 mm in total length and 35 mg live weight were introduced when a noticeable bloom of phytoplankton first appeared. The interval between inoculating and fertilizing and the introduction of fry varied from 3 to 12 days. Inability to find the expected numbers of fry after they were introduced led to the assumption that mortality had occurred in some of the 310-liter microcosms. Because it was sometimes impossible to find the expected numbers of fry after their initial introduction, it was assumed that they had died and more were added. Subsequent counts showed that this was not so and the surplus fry were removed. Populations in most of the 310-liter series were adjusted to five before the end of the experiment. The fish population in microcosm 2 was reduced to three by starvation, while those of 7 and 8 were intentionally reduced to three when the projected rate of fish biomass increase suggested an impending effect on their growth by accumulating metabolites. The high population densities in experiments 9,

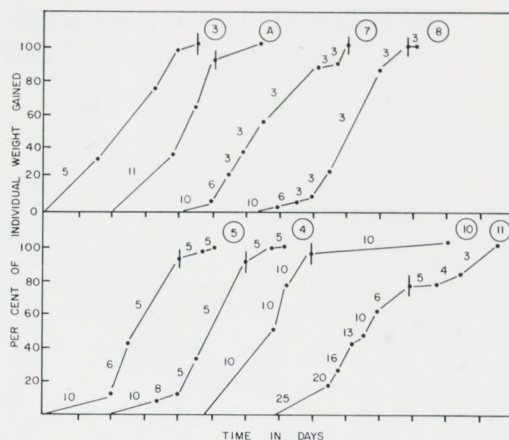


FIG. 2. Relative growth rates of *T. mossambica* in experiments where progressive growth records were kept. Circled figures are experiment numbers. Numbers not circled indicate total population present during period indicated by adjacent line segment. Vertical lines indicate end of rapid growth phase used in Fig. 1. Each division of the horizontal scale equals 20 days.

10, and 11 were used to discern effects of competition.

Light

The tanks were placed in direct sunlight. Experiments were conducted either during April, May, and June or during July, August, and September. Each tank was provided with a transparent plastic cover that was frequently washed free of dust. Covers were sufficiently tight to exclude most dust.

Turbulence and pH

Slight mixing was induced by gentle aeration, which was approximately equal for each tank. A tendency to use carbon dioxide faster than it could be regenerated or absorbed from the atmosphere was corrected by slightly enriching the air picked up by the aerator pumps with this gas. An attempt was made to keep pH between 7.0 and 8.0 by regulating the carbon dioxide content of the air pumped in. The desired pH range was maintained most of the time, but values as low as 6.5 and as high as 10.0 occurred.

Temperature

Temperatures were moderated by flowing well water through a metal jacket sur-

[1965]
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926
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The Phosphorus Content of Some Aquatic Macrophytes with Special Reference to Seasonal Fluctuations and Applications of Phosphate Fertilizers

by

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(with 1 fig.)

INTRODUCTION

This study constitutes part of an investigation into the effects of added phosphatic fertilizers on the productivity of certain shallow, relatively unproductive freshwater lochs in the highlands of Scotland. Aquatic macrophytes are an important component of some of the lochs under investigation and may play a significant part in determining the fate of any nutrient added.

Existing information on the chemical composition of aquatic macrophytes is rather scanty. The papers of SCHUETTE & HOFFMAN (1922) and SCHUETTE & ALDER (1927, 1929) provide valuable data on the composition of the aquatic plant species which occur in Lake Mendota and Green Lake, Wisconsin. HARPER & DANIEL (1934) analysed the aquatic vegetation of ponds and lakes in Oklahoma for phosphorus, nitrogen and calcium, and MISRA (1938) recorded the results of analyses of aquatic plants from the English Lake District. More recently, WEATHERLY & NICHOLLS (1955) have made observations on the higher aquatic vegetation of a highland lake in Tasmania following artificial enrichment with a mixed fertilizer. They carried out analyses of *Myriophyllum elatinoides* to gain information on the effect of the fertilizer on plant growth and noted that, in the year following the addition of the fertilizer, a distinct pattern of

clumps of *Myriophyllum elatinoides* appeared, growing along the lines of the traverses made when the bags of fertilizer were dropped in the lake. The fertilizer was applied to about half the total surface area of the lake. The number of *Myriophyllum* plants, assessed by counting the number of heads above the water surface, was very small prior to enrichment. After fertilization, a considerable increase in this species was recorded and it was noted that plants from the enriched area of the lake had a much greater phosphorus content than those from the unenriched areas. It should be mentioned that in the papers referred to above, with the exception of that by HARPER & DANIEL, the time of harvesting is not recorded.

It is essential to know the extent of normal seasonal fluctuations in the phosphorus content of plant tissues before an assessment can be made of any changes following fertilization. The studies described in this paper were undertaken for this purpose.

SAMPLING AND ANALYTICAL METHODS

Preparation of Plant Material

Plants from shallow water were collected by hand, while those in deeper water were obtained by means of a grapnel trailed from a small boat. They were immediately placed in polythene bags and, on return to the laboratory, were thoroughly washed under a jet of water in order to free them from any attached organisms such as insect eggs or larvae, algae etc. The samples were then dried at 60°C for a minimum period of 24 hours, powdered in a mortar and stored in glass specimen tubes.

Method of Analysis

Phosphorus was determined colorimetrically, following wet digestion with a perchloric acid/nitric acid mixture, by a modified form of the SHERMAN (1942) method. Approximately 0.05 g of powdered sample was digested with 4 ml 60% perchloric acid (commercial grade) and 1 ml concentrated nitric acid (A.R. grade) at 120°C for 4 hours. After cooling, approximately 20 ml of distilled water were added and the flasks were replaced on the hot-plate for a further 15—20 minutes to convert any pyro- and meta- phosphates to orthophosphate.

An aliquot of the digest (normally 5 ml), mixed with 5 ml of ammonium molybdate (50 g/l) and 4.6 ml 6 N sulphuric acid was treated with 1 ml of the reducing solution (0.59 g 1.2.4-amino-naphthol-

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EFFECTS OF REDUCED AND PERTURBATED FLOW BELOW DAMS ON FISH FOOD ORGANISMS IN ROCKY MOUNTAIN TROUT STREAMS

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ABSTRACT

The alteration of flow regimes resulting from stream regulation may greatly modify the density, biomass, diversity, and species composition of fish food organisms in the tailwater reaches below dams. Important taxonomic or functional groups of lotic benthos are often rare or absent in the receiving stream. Life cycle phenomena and the trophic structure of the benthic community may also be transformed by direct and indirect effects of flow regulation. Recovery from temporary adverse conditions is greatly delayed since "drift," a major recolonization mechanism of stream benthos, is blocked by the upstream lentic environment. The degree and type of biotic modifications engendered by flow alterations are a function of (1) the extent of discharge alteration, (2) the periodicity of the altered pattern, (3) the relationship of periodicity and season, (4) synergistic effects (e.g., thermal-flow relationships), and (5) site-specific factors. Data from regulated Rocky Mountain trout streams are presented to elucidate the interrelated factors responsible for qualitative and quantitative alterations of the benthic communities below dams. Flow regime modifications include reduced flow from interbasin diversion, perturbed flow patterns with diel periodicities, enhanced seasonal flow constancy associated with diel fluctuation, and severe arrhythmic fluctuations.

RÉSUMÉ

L'altération des régimes résultant de la régularisation des cours d'eau peut modifier substantiellement la densité, la biomasse, la diversité et la composition par espèces des organismes dont se nourrissent les poissons dans les biefs situés en aval des barrages. D'importants groupes taxonomiques ou fonctionnels du benthos lotique sont souvent rares ou absents dans le cours d'eau récepteur. Les phénomènes relatifs aux cycles biologiques et à la structure trophique de la communauté benthique peuvent également être modifiés par les effets directs et indirects de la régularisation du débit. Le rétablissement faisant suite à des conditions contraires temporaires est souvent retardé, car "la dérive"—principal dispositif de recolonisation du benthos fluvial—est bloquée par l'environnement lentique d'amont. Le type et l'ampleur des modifications biotiques engendrées par les altérations du débit sont fonction de: 1) l'amplitude des altérations; 2) la périodicité du mode d'altération; 3) le rapport entre la périodicité et la saison; 4) les effets synergiques (par exemple, les rapports température-débit); et 5) les facteurs de spécificité du site. Les auteurs présentent des données ayant trait aux rivières à truites régularisées des Montagnes Rocheuses pour mettre en lumière la corrélation entre les facteurs responsables des altérations qualitatives et quantitatives des communautés benthiques en aval des barrages. Les modifications des régimes comportent la réduction du débit par suite de dérivations entre bassins, les perturbations du réseau d'écoulement associées aux périodicités nyctémérales, le raffermissement de la constance du débit saisonnier associé aux fluctuations nyctémérales, et de fortes fluctuations arythmiques.

INTRODUCTION

The myriad hydrological, limnological, geochemical, meteorological, and biological factors affecting ecological conditions in regulated

streams have recently been described in the proceedings of the First International Symposium on Regulated Streams (Ward and Stanford 1979a). Since 1972, we have studied the effects of stream regulation on a variety of trout streams

in the Rocky Mountains. The lotic systems investigated occur at different elevations and are influenced by impoundments with various operational schemes and managerial objectives.

It is the purpose of this paper to briefly summarize the effects of reduced and perturbed flow on fish food organisms in regulated Rocky Mountain trout streams. The effects of other factors, such as temperature modification, resulting from stream regulation have been dealt with elsewhere (e.g., Ward 1976a; Ward and Stanford 1979b).

FLOW REGIME ALTERATIONS

Reduced flow below dams, compared to historical discharge, may occur for a variety of reasons. Within-basin diversions, such as irrigation withdrawal from reservoirs, may reduce discharge below dams. In some instances, the majority of water released from the reservoir is transported by conduit to a downstream powerhouse, thus bypassing a section of the stream. Modification of the annual flow regime by regulation may result in periods of abnormally low flow even though the yearly discharge remains the same. Annual discharge may, however, be significantly reduced by increased evaporative loss from impoundment.

Perhaps the most dramatic reductions in flow are associated with interbasin diversions. In Colorado, major transmountain diversion schemes carry water through tunnels under the Continental Divide (Stanford and Ward 1979), resulting in great reductions in flow in some stream systems and increases in others.

Tailwaters below hydroelectric dams characteristically undergo severe short-term periodic flow perturbations as a function of temporal variations in power demand. Such short-term flow fluctuations may be associated with en-

hanced seasonal flow constancy relative to preimpoundment discharge patterns.

Downstream demands for water for agricultural, industrial, and domestic uses may result in great short-term variations in discharge below storage and irrigation reservoirs, although without a well-defined periodicity.

Three regulated Rocky Mountain trout streams will be used in this paper to exemplify three types of flow regulation (Table 1). Impoundment and transmountain diversion of upper Colorado River water reduced annual discharge below Granby Dam, Colorado, to only 11% of the historical flow (Weber 1959). Prior to diversion, mean annual discharge was 9,1 m³/sec with monthly means ranging from 1,0 (February) to 38,6 (June). Following closure of the dam, a stepwise flow schedule was established in which 0,6 m³/sec was released from September through April, 2,1 m³/sec May–July, and 1,1 m³/sec during August. The South Fork of the Flathead River near Glacier National Park, Montana, exhibits severe diel flow fluctuations, associated with enhanced seasonal flow constancy, due to hydroelectric generation. Discharge may range from 7,5–260 m³/sec in a single day (Fig. 1). Joe Wright Creek, a high mountain stream in northern Colorado, exhibits great short-term fluctuations in discharge without a well-defined periodicity, due to erratic releases from an irrigation reservoir (Ward and Short 1978). At low flow, pools and riffles alternated and the stream averaged 5 m in width; at high flow, the stream was about 17 m wide without an apparent pool-riffle sequence. During extreme periods of low discharge, surface flow was barely discernible. Although varying in size and type of regulation, the three lotic systems described above are all cold mountain streams with relatively soft waters and stony bottoms. All were virtually unimpacted except by regulation.

Table 1. Regulated Rocky Mountain trout streams which exemplify three types of flow regime alterations (see text).

Stream system	Upstream reservoir	Storage capacity ^a hm ³	Elevation m a.s.l.	Flow m ³ /sec	Flow alterations
S.F. Flathead River	Hungry Horse	4 276	1 085	7,5–260 ^b	Diel fluctuation
Colorado River	Granby	666	2 460	0,99 ^c	Flow reduction
Joe Wright Creek	Chambers	11	2 765	0,01–9,79 ^d	Arrhythmic fluctuation

^a hm³ = cubic hectometers.

^b Maximum daily variation.

^c Annual mean discharge, 11% of historical flow (Weber 1959).

^d July–November, 1975.

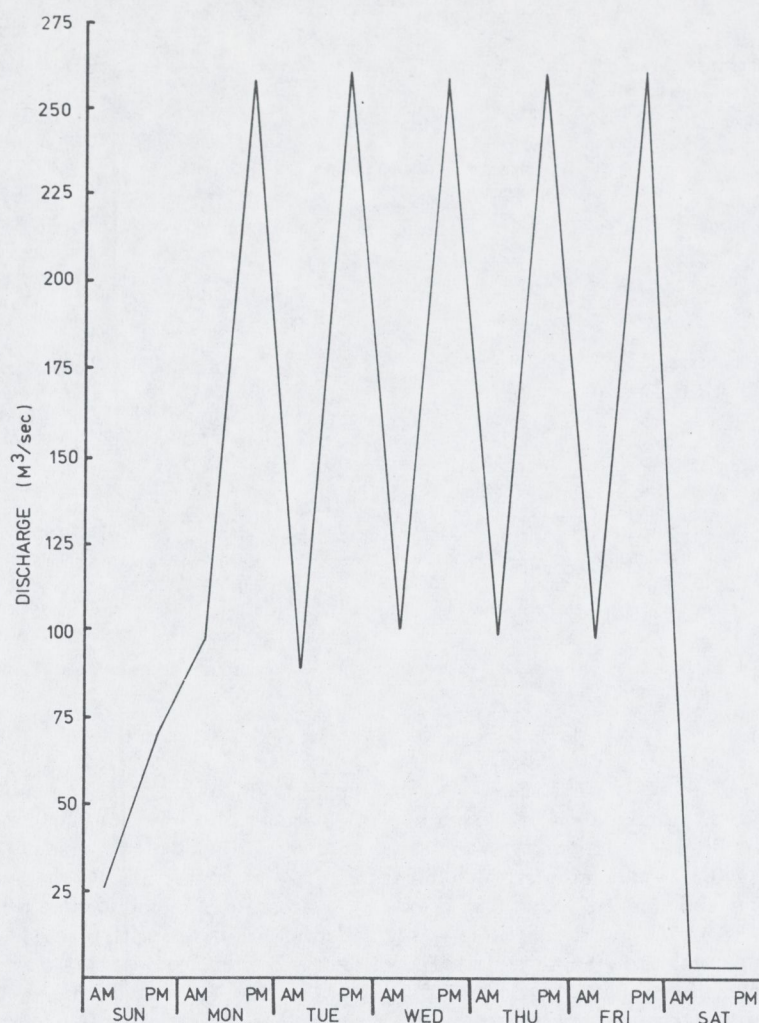


Fig. 1. Hourly discharge from Hungry Horse Reservoir on the South Fork of the Flathead River, Montana, 9-15 October 1977.

GENERAL EFFECTS ON BENTHOS

Reduced and perturbed flow below dams have a variety of subtle and direct effects on stream benthos mediated through a complex series of interrelated responses of the stream ecosystem to altered conditions. Following a description of qualitative and quantitative effects of reduced and perturbed flow on stream zoobenthos, causal interrelationships will be examined.

Some general biological responses to different types of stream regulation are shown in Table 2. It is not implied that all biotic alterations below

dams are flow related. Some, for example, are clearly the result of thermal alterations (Ward and Stanford 1979b). However, the thermal regime may be significantly influenced by the discharge pattern as discussed later.

Macroinvertebrate density and biomass values were only slightly reduced by arrhythmic flow fluctuations below the reservoir on Joe Wright Creek. Even above the reservoir, the generally harsh conditions in this high elevation, soft water stream are manifested in a low standing crop of benthos. However, macroinvertebrate composition was dramatically different below the dam. Only gross composition changes

Table 2. Macroinvertebrate standing crop and taxonomic alterations associated with stream regulation in Rocky Mountain trout streams.

		Macroinvertebrates			Salmonids present ^b
		Density number/m ²	Wet biomass g/m ²	Composition changes ^a	
Joe Wright Creek	Above reservoir	1 476	3,9	Ephemeroptera-S Plecoptera-S	<i>Salmo gairdneri</i> <i>Salmo clarki</i>
	Below reservoir			1 259	2,5
Colorado River	Sep. 1949 (preimpound.)	1 610	22,6	Ephemeroptera-S Plecoptera-D	<i>Salmo gairdneri</i> <i>Salmo trutta</i>
	Sep. 1957 (postimpound.)	2 165	6,5	Trichoptera-D Diptera-I	<i>Salvelinus fontinalis</i>
	Sep. 1978 (postimpound.)	5 223	12,0	Oligochaeta-I,D	
Flathead River	Middle Fork (unregulated)	2 950	6,0	Ephemeroptera-D Plecoptera-D	<i>(Oncorhynchus nerka)</i>
	South Fork (regulated)	2 490	1,5	Trichoptera-D Diptera-I Oligochaeta-I	

^a Symbols: S = similar, I = increase, D = decrease in relative abundance (numbers) in regulated, compared to unregulated, sections.

^b In regulated reaches.

are indicated in Table 2; more detailed description is necessary to examine the possible reasons for alterations in the community structure. Thus, while mayflies (Ephemeroptera) exhibited similar relative abundance above and below the reservoir on Joe Wright Creek, there was a shift from a predominantly heptageniid mayfly community (69% of mayflies) to a *Baetis* dominated (97% of mayflies) assemblage below the dam. Stoneflies (Plecoptera) shifted from nemourids (55%) to chloroperlids (98%). Other workers have also reported a relative enhancement of chloroperlid stoneflies in streams with widely fluctuating flow regimes (Radford and Hartland-Rowe 1971; Trotsky and Gregory 1974). Surprisingly, caddisflies (Trichoptera), although reduced by regulation, did not exhibit any dramatic shifts in composition. The dipteran community changed from one dominated by chironomids to a chironomid/simuliid assemblage. Oligochaetes were only collected in the stream section below the reservoir. The stream below the dam was characterized by fewer species and a less even distribution of taxa.

Benthos in the upper Colorado River below Granby Dam was studied by the U.S. Fish and Wildlife Service in 1949 prior to impoundment, and in 1957 (Weber 1959) and 1978-9 (Ward,

unpubl.) following impoundment. Data from September (the only month common to all three studies) are shown in Table 2. A progressive increase in numbers is shown since 1949 when the stream was impounded and the majority of the water diverted to the east side of the Continental Divide. Biomass shows a reduction from 1949 to 1957, followed by an increase, but not to preimpoundment levels. A comparison of biomass and numbers indicates a much smaller individual size for the species present after impoundment. Small mayflies (*Baetis*), chironomids, simuliids, and initially oligochaetes dominated the regulated stream benthos. Stoneflies have been virtually eliminated and caddisflies have been greatly reduced. Food habits of rainbow trout *Salmo gairdneri* sampled during the summers of 1949 and 1957 (Weber 1959) reflected the alterations in the benthic composition during that period except for two major exceptions. The great increases in dipterans and oligochaetes were not reflected in the food habits of rainbow trout, indicating the lesser value or availability of these invertebrates as food items. Trout collected in 1949 generally had higher condition factors than those collected in 1957. Crisp et al. (1978) found that the stomachs of brown trout *Salmo trutta* below a dam in Eng-

land contained more mayflies and chironomids but fewer terrestrial insects than prior to regulation. Baetid mayflies increased in abundance in trout stomachs relative to heptageniid mayflies, which reflected the composition of the regulated river benthos.

The reduced flows below Granby Dam were not sufficient to remove sediment which accumulated during dam construction. Bottom samples taken shortly after impoundment (Eustis and Hillen 1954) revealed more dramatic changes in stream benthos than those shown in Table 2. To ameliorate the sediment accumulation, a large volume of water (1224677 m³) was released from Granby Dam during 15-18 April 1952 to simulate spring runoff which had been eliminated by regulation. The flushing operation reduced average sediment depth in pool areas from 3.5 to 1.2 cm. Maximum sediment removal occurred in riffle areas. While considered highly successful in improving the habitat for trout and fish food organisms, to our knowledge such simulated runoff conditions have not been repeated, although flood waters have topped the spillway on rare occasions.

A striking feature of the Flathead River system is the phenomenal diversity of aquatic insects in unregulated reaches (Stanford and Gaffin, in press; Hauer and Stanford, unpubl.). Only stoneflies (42 species) and caddisflies (38 species) have been intensively studied. Until additional samples including the total macroinvertebrate community are analyzed, the exact standing crop values in Table 2 should be regarded as preliminary. The general pattern, however, is clear: a considerable reduction of biomass in the regulated South Fork associated with density values not dissimilar to those of the unregulated Middle Fork. Of the 42 species of stoneflies, only 5 small-bodied species are found (in low numbers) in the South Fork. Caddisflies are virtually eliminated below the dam; the majority of samples collected do not contain a single trichopteran. The mayfly fauna of the South Fork is composed almost exclusively of small *Baetis* nymphs; 35 species, dominated by heptageniids, occur in the Middle Fork. Riffle beetles have been eliminated below Hungry Horse Dam (and below Chambers Lake). Approximately 130 species of aquatic insects occur in the Middle Fork, of which only 15 have been collected in the regulated South Fork where from 95-99% of the fauna is comprised of chironomids and oligochaetes. Although a few

kokanee salmon (*Oncorhynchus nerka*) migrate into the South Fork from Flathead Lake, other salmonids (*Salmo clarki*, *Salvelinus malma*) are absent.

CAUSAL INTERRELATIONSHIPS

The majority of factors responsible for alterations of fish food organisms, which directly or indirectly result from flow modifications in regulated streams, may be conveniently discussed under (1) substrate-flow relationships, (2) current-flow relationships, and (3) temperature-flow relationships.

Substrate-Flow Relationships

Reduced and fluctuating flow regimes both drastically alter the substrate with important effects on stream benthos. Siltation resulting from reduced flow, especially if the flushing action of spates and major periods of runoff are lacking, has direct and subtle effects on the benthic community. Quality food organisms such as mayflies, stoneflies, and caddisflies are generally reduced, whereas burrowing species of oligochaetes and chironomids are favored. The density of benthos may increase, although the size of individual organisms and their availability as food items normally decrease. Silt reduces interstitial spaces, current velocity, and oxygen levels in the hyporheic zone, thus decreasing the value of the substrate as an incubation site for salmonid eggs and fry, and as a population reservoir for benthic invertebrates. Reduced flow tends to reduce substrate heterogeneity and the suitability of habitat for erosional zone zoobenthos. Such conditions may, however, favor aquatic angiosperms and allow establishment of organisms (e.g., amphipods, snails, tricorythid mayflies) not normally present in high gradient mountain streams. Algal growth may also be enhanced under conditions of increased water clarity and reduced bank and bed erosion. Algal densities may reach nuisance levels in the Colorado River below Granby Dam during long periods of low, constant discharge. Benthic species requiring clean rock surfaces may be eliminated, even without excessive siltation, by dense populations of epilithic algae, which may partly explain the reduction of heptageniid mayflies below dams (Ward 1976b).

Low, constant flow may allow encroachment of riparian vegetation to the detriment of fishes and benthos or may result in the establishment

of nonriparian species along the stream banks. Under certain conditions, the elimination of silts and clays, due to the clarifying effect of an upstream reservoir, may decrease the moisture-holding capacity of newly-formed banks and thus prevent colonization by riparian vegetation (Simons 1979). Streamside vegetation has major thermal, trophic, and hydrologic ramifications for lotic systems. Any modification of the density or composition of the riparian habitat by flow regime alterations (or other factors) will have important effects on the stream ecosystem.

As discharge is reduced, the substrate areas most productive of fish food organisms are the first to be exposed. Below Granby Dam a reduction of discharge from 2,8 to 0,6 m³/sec decreased the most productive areas of stream bed from 59 to 18%, respectively (Weber 1959).

Successive releases of sediment-free water from Hungry Horse Reservoir have resulted in an armored and cemented substrate below the dam. The hyporheic habitat, so extensive in other portions of the Flathead River system (Stanford and Gaufin 1974), has been eliminated by flow regulation. In contrast, the arrhythmic flow fluctuations below Chambers Lake, while greatly reducing nemourid stoneflies and heptageniid mayflies, has increased the relative abundance of chloroperlid stoneflies. This latter group consists of small linear species apparently able to tolerate periods of extreme low flow by burrowing into the substrate (Ward and Short 1978). The distributions and abundance of sedimentary detritus, which influences stream productivity (Rabeni and Minshall 1977), must be greatly modified by flow perturbation, but few data are available. The reduction of nemourid stoneflies (large-particle detritivores) below Chambers Lake may be due to the reduction of their habitat (accumulations of leaf litter) by rapidly fluctuating discharge.

Taxonomic variations in susceptibility to stranding and tolerance to exposure also selectively eliminate benthic species in streams with rapid flow fluctuations (Brusven et al. 1974). Chironomids appear most tolerant, whereas mayflies are most severely affected by stranding and exposure. A heterogeneous substrate provides some refuge for benthic species during both low and high water periods.

Current-Flow Relationships

Benthic species may have very specific current velocity requirements associated with feeding

mechanisms or respiratory physiology (Hynes 1970). Short-term flow perturbations may eliminate species restricted to pools as well as those adapted to rapid water. Requirements for a given substrate type may also restrict benthic macroinvertebrates to a specific range of current velocity.

The phenomenon of invertebrate "drift" is an important functional attribute of lotic ecosystems (Waters 1972). Drift is a major recolonization mechanism and drifting invertebrates provide a major source of food for stream salmonids. Catastrophic drift may be induced by increases or decreases in discharge (Anderson and Lehmkühl 1968; Minshall and Winger 1968), which may conceivably permanently reduce faunal density if recolonization from upstream is blocked by a reservoir. Since propensity to drift is species specific, catastrophic drift without compensatory recolonization would result in significant shifts in community structure.

Thermal-Flow Relationships

The extent to which the thermal characteristics of water released from a dam influence downstream reaches is directly related to discharge. Small volumes of water more rapidly equilibrate with ambient air temperatures if a thermal differential exists. Reduced flow below dams may therefore result in elevated summer water temperatures and extreme ice conditions in winter.

Fluctuating flow patterns in the South Fork of the Flathead River below a deep-release dam result in an expanded and desynchronized diel thermal pulse in the mainstream river in the summer (Fig. 2). During periods of high discharge associated with power generation, cold water is carried great distances downstream, whereas high summer air temperatures rapidly modify water temperatures during low flow periods. A sudden drawdown during the winter of 1973 caused massive mortality of stonefly nymphs in the mainstream Flathead River (Stanford and Ward 1979). These winter species which had congregated in shoreline areas prior to emergence were killed when reduced flow permitted icing conditions in shallow waters. During the same year the stonefly *Claassenia sabulosa* failed to emerge because increased late summer discharge from Hungry Horse Reservoir depressed mean daily temperatures below 18°C, thus failing to provide an appropriate thermal cue (Stanford and Gaufin, in press).

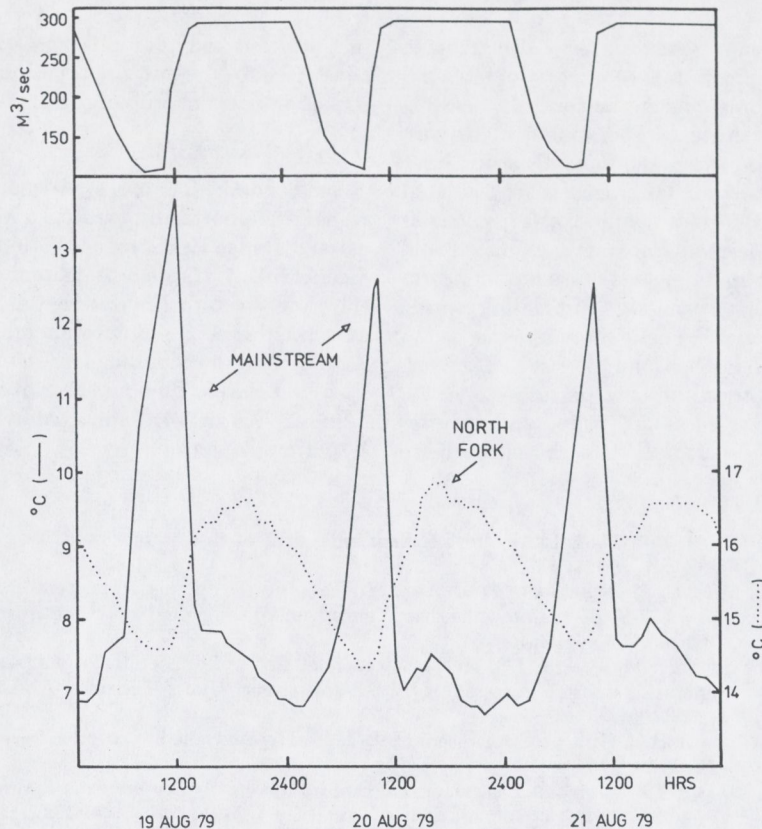


Fig. 2. Relationship between discharge and temperature in the Flathead River system, Montana. The upper curve shows discharge in the mainstream river below the confluence of the South Fork. The South Fork, which is regulated by a deep-release hydrogeneration facility, contributes an average of 37% of the mainstream flow. The diel pulses of cold water and intervening periods of low flow greatly modify the summer thermal regime of the mainstream river, which is contrasted with the unregulated North Fork on the lower curve. Diel fluctuations in discharge expand the thermal range and temporally displace the diel temperature pattern.

Thermal factors may provide a major influence on the processing of detritus in regulated streams despite reductions in allochthonous inputs and shredder species (Short and Ward 1980).

CONCLUSIONS

The biota of streams have evolved in response to natural variations in the flow regime. Spates, peak periods of seasonal runoff, and major long-term flow events (floods) have shaped the evolutionary history of lotic organisms and lotic ecosystems. For example, Hayden and Clifford (1974) describe a mayfly which uses seasonal flow variations as migration cues during different life cycle stages. It is, therefore, not surprising that major alterations in discharge patterns are manifested by severe modifications of the

stream community. Some types of stream regulation mimic conditions in special lotic habitats. Thermal and flow constancy in tailwaters below some deep-release storage reservoirs present conditions similar to those prevailing in springbrooks, and the biota respond accordingly (Ward and Short 1978). Other operational schemes have no natural analog. Only certain glacier-fed streams, which each day during summer change from raging torrents to mere trickles, exhibit anything resembling the severe diel flow perturbations characterizing streams below hydroelectric power dams. Species which have "estival" life cycles may be better adapted for conditions in regulated streams with severe short-term flow perturbation than "hiemal" species (Henricson and Mueller 1979).

Although biotic communities are invariably

altered by stream regulation, and although the extent of modification is a function of site specific factors, some managerial control is feasible within the stricture of operational objectives. Extremely productive salmonid fisheries have been maintained for long periods in regulated streams under certain conditions (see e.g., reference to Cheesman Canyon in Stanford and Ward 1979). Much depends on maintaining environmental heterogeneity. Simulating spring runoff may greatly benefit some streams as described for the upper Colorado River. Decreasing the abruptness of flow perturbations will lessen stranding losses of fishes and invertebrates. Extant ecological data should be more

fully utilized and additional research should be conducted for the purposes of minimizing downstream impacts of stream regulation projects.

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